DOCTOR OF PHILOSOPHY

Applications of spatial game theory to host-parasitiod interactions an individual-based modelling approach

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University of Dundee

Applications of Spatial Game Theory to Host-Parasitiod Interactions: An Individual-based Modelling Approach

By

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To Anluain and to my parents for their constant support and encouragement.

Contents

Declaration

I declare that the following thesis is my own composition and that it has not been submitted before in application for a higher degree.

Andrew Edward Felix Burgess

Certification

This is to certify that Andrew Edward Felix Burgess has complied with all the requirements for the submission of this Doctor of Philosophy thesis to the University of Dundee.

Prof. Mark Chaplain

Certification

This is to certify that Andrew Edward Felix Burgess has complied with all the requirements for the submission of this Doctor of Philosophy thesis to the University of Dundee.

Prof. Steve Hubbard

Quotation

”*What? Do we really want to permit existence to be degraded for us like this-reduced to a mere exercise for a calculator and an indoor diversion for mathematicians? Above all, one should not wish to divest existence of its rich ambiguity*”

Friedrich Nietzsche, *The Gay Science*.

Chapter 1

Introduction

The evolution of cooperation has been a fundamental and controversial problem in biology. Darwin's response was to posit a mechanism of group selection. This has remained controversial right to the present time. Indeed one of the motivations for the development of evolutionary game theory was to counter group selections claims that certain display traits had evolved to avoid lethal combat for the good of the species. It is perhaps ironic therefore that scholars have subsequently turned to the same evolutionary game theoretic structure to ask for a resolution of the issue of the evolution and sustainability of cooperation. That cooperation occurs in nature is undeniable. From the components or eukaryotic cells, to assemblages of cells themselves into metazoans to social cooperation in animals and indeed human societies. In the case of human cooperation, it has been suggested that one very visible manifestation of our socially cooperative heritage can be seen in our eyes themselves. Humans have a large and distinctive white area in their eyes, the sclera, that is shared by no other primate. The obvious effect of the sclera is to make obvious the direction of ones gaze, and while that might be a disadvantage in most primate societies where direct gaze is threatening and intimidating, in early human hunter gatherer communities it would have facilitated

the silent communication of the object of ones attention and signalled directional information. Such silent comunication would have been useful in a hunting scenario [126], [127], [128], [129], [130].

The title of this thesis derives from the initial motivation of this work, which was to develop the work of Chaplain, Schofield and Hubbard on host-parasitoid interactions. Parasitoids are insects (dipterans or hymenopterans) which do deposit their eggs within the living bodies of of arthropod larvae (usually lepidopterans). The system upon which I was engaged to work involved a wasp parasitoid (Ichneumonidae or Cotesia glomerata) upon a butterfly larvae (such as Pieris brassicae), see for example [26]. Host-parasitiod interactions are a major theme in arthropod interactions and parasitoids themselves are estimated to constitute some ten percent of all metazoan species [133]. During the course of this work, a detailed simulation program was produced modelling the interaction of host larvae and wasp parasitoids and their developing eggs. In thinking about how best to analyse these interactions some effort was spend on attempting to determine an applicable game theory structure. This was not an easy task, and it was then realized that it would actually be far easier to model game theory interactions between agents on a grid directly. To do this much of the complicated model machinery to do with incubation times, parasitoid searching efficiency etc was jettisoned. The resulting model of game theory interaction is what constitutes the work presented in this thesis.

We begin with a discussion of the original motivation and application of game theory to problems of human decision making and societal choices. We draw some conclusions as to the applicability of game theory to these issues before moving on to examine applications of game theory to evolutionary problems. The final section contains a brief review of more recent literature in this area and also outlines the motivation for the main problem addressed in this thesis.

1.1 Game Theory and Human behaviour

The theory of games was first formalized by John von Neumann and Oscar Morgenstern in their 1953 book 'The Theory of Games and Economic Behaviour'. [1] As a model of human economic behaviour, classical game theory makes some assumptions that are required for ease of analysis, but which may not actually be true of all real human actions in all cases. Classically, players are assumed act according to their own self-interest which is to maximise their own payoff. To that end players are assumed to be rational, and they must also assume that their fellow players also be rational. In fact, there is an infinite regress here, for all must assume that: the players are rational, that all the players know that all the other players are rational, and that all players are aware that all the players are aware that they are all rational, and so on ad infinitum. This chain of assumptions is denoted the Common Knowledge of Rationality, or CKR. Whilst considerably simplifying analysis, such an assumption is often in conflict with results of experimental studies that place human volunteers in a game theory scenario. [55]

The development of game theory was motivated by the desire to find a mathematical method to analyse human decision making and human conflict. It originates therefore in the belief that mathematical analytical thinking should determine, or at least inform, the solutions to human societal problems. Among the architects of game theory were those such as John von Neumann, who believed strongly in an aristocracy of the intellect and in the technocratic management of society. Von Neumann held numerous government consultancy roles and was also employed by the RAND Corporation. The RAND Corporation was set up by the United States Airforce, and became instrumental in the analysis and recommendation of strategies applicable to global nuclear conflict. The doctrine of nuclear deterrence by mutually assured destruction (MAD) is largely

credited to work at RAND. Several employees and consultants at RAND were influential in the development of game theory, including the inventors of the Prisoners' Dilemma, Merril Flood and Melvin Dresher. Interest in game theory was therefore closely linked to cold war tensions regarding the management of conflict.

The Prisoners' Dilemma has been called the "central issue of defence". Indeed, in its iterated form it is sometimes otherwise known as the "Peace-War" game. With regard to nuclear proliferation the issue is whether to gain security for oneself at the expense of the common good. As is well known, the Nash equilibrium for a (single round) Prisoners' Dilemma is to defect. This does not augur well for those wishing to establish the rationality of avoiding a nuclear arms race. Perhaps not surprisingly, von Neumann's own attitude to nuclear proliferation was consistent. He regarded defection as unavoidable and eventual conflict inevitable and in fact publicly favoured a surprise first strike against the USSR. In an interview published in Life magazine, von Neumann is quoted as saying: "If you say why not bomb them tomorrow, I say why not today?" [Quoted in [2]]. Perhaps it should be of concern that senior government advisors held such bellicose opinions. But at the time this was not an extreme view. Bertrand Russell was also arguing publicly in support of a "preventative war" in which a coalition led by the USA was to issue a nuclear backed ultimatum to the USSR to submit to a world government dominated by the United States. In the face of such nuclear blackmail, Russell held the opinion: "I am inclined to think that Russia would acquiesce; if not, provided this is done soon, the world might survive the resulting war and emerge with a single government such as the world needs." [Quoted in [2]].

It was therefore the considered opinion of influential and intelligent people that the solution to the issue of nuclear proliferation was to provoke the very conflict that they professed they so wished to avoid. Furthermore, Russell, von Neumann and those at RAND viewed the matter as one of logic, and their solution as rational. In Russell's case this is all the more astonishing given his otherwise renowned humanity.

Russell was himself a distinguished logician and so presumably was well aware of the full sense of his own words when he remarked regarding his support for preventative war that ”The argument I have been developing is as simple and as inescapable as a mathematical demonstration” [Quoted in [2]]. If there is a lesson here, it is that one should beware of all proclamations pretending to mathematical certainty, or any species of certitude for that matter, in the arena of human relations.

However, even at the start there was some evidence that such confidence in ”inescapable” rational conclusions might, after all, be misplaced. In their first paper on the Prisoners' Dilemma entitled ”A Non-Cooperative Pair”, Merril and Flood reported their experimental investigations of the game. In one hundred trials, their subjects attempted repeatedly to establish cooperative behaviour, with one player choosing to cooperate sixty eight times and the other seventy eight times out of a hundred. Puzzled that the obvious Nash equilibrium was not a popular choice of action, the authors approached John Nash himself. Nash responded that the correct way to view the trial was not as one hundred separate interactions, but as one large multi interaction game. However, this did not in fact resolve the issue, for it turns out that even in such repeated interactions, the equilibrium situation is for both players to defect in all one hundred rounds of the game. Subsequent work has demonstrated that in human trials subjects display a systematic bias towards cooperative behaviour. [48], [49] Humans therefore seem to have no instinctive preference for the Nash equilibrium. As Poundstone has remarked: ”Well over nine tenths of the applications of game theory purport to describe or predict human behaviour. But game theory is not very good at predicting what people will do.” Does this mean that ultimately human beings are not rational beings?

One-time RAND consultant and Nobel laureate in Economics, Thomas Schelling, notes in connection with the mathematical solution of game theory scenarios:

”We must avoid assuming that everything the analyst can perceive is perceived by the

participants in a game. In particular, game characteristics that are relevant to sophisticated mathematical solutions might not have [the] power of focussing expectations and influencing the outcome...If the phenomenon of ”rational agreement” is fundamentally psychic - convergence of expectations - there is no presumption that mathematical game theory is essential to the process of reaching agreement, hence no basis for presuming that mathematics is a main source of inspiration in the convergence process.” [10]

Which is to say that the structures of thought and convention used in human decision making in game scenarios may not be wholly amenable to purely mathematical analysis.

Incidentally, another problem with the applicability of game theory to human affairs is the issue of the strict definition of utilities. In order for the game theorist to have any basis for his calculations, for him to have numbers to work on, the desirability of all possible outcomes must be placed on a strict numerical scale. But how is this to be done in practice? Utility has no units and cannot be measured in the manner of a physical property. For sure, one may have confidence to assign numbers to outcomes such as global war, but the entire motivation for studying game theory was that it should provide for recommendations more accurate than intuition. But if the underlying utilities are assigned by intuition then the claim of game theory to objectivity must be considered to be somewhat attenuated. For opinions and intuitions regarding orders of rank will often vary among people in matters of any complexity.

Others have sought, sometimes with the hopeful ingenuity of the theologian, to demonstrate that cooperation is the rational choice for individual action after all. There have been numerous attempts to derive cooperation as a rational consequence of Prisoners' Dilemma type situations, some more contorted than others. One interesting and influential aspect of this work has been the focus on the Iterated Prisoners' Dilemma.

Axlerod's tournamants, which we shall discuss in the next section.

Attempts to derive cooperation from the Prisoners' Dilemma as a consequence of rationality alone have difficulty. This is because even at the simplest level of repeated Prisoners Dilemma trials, evidence has existed for a long time that human beings are more cooperative than rationality or rather game theory analysis should expect. Game theory turns out not to be a good predictor of human behaviour. A natural conclusion to draw would therefore be that game theory so constituted is not an appropriate tool by which to model human behaviour. As humans just do not conform well to the predictions of game theory we might do well to seek an explanation for the human bias towards cooperation.

As well as capturing the central issue of defence, the Prisoners' Dilemma is seen by some as reflecting the central problem of society. The essential conflict in such Prisoners' Dilemma situations is between ones own private gain (defection) and the greater common good (cooperation). It is between individual and collective rationality. As such, some regard it as a metaphor for the social contract. Without a social contract, there is a natural state of anarchy or lawlessness, what Hobbs called the war of all against all, a state in which life is "solitary, poor, nasty, brutish and short" . [4] This corresponds to the case in which all players, following their individual self interest, choose defection over cooperation. Hobbes argued that the imposition or acceptance of a social contract should be envisaged as a collaborative, cooperative act, resulting in improved conditions for all. But this underpinning cooperative step may itself be irrational.

Prisoners dilemmas occur whenever self interest is opposed to group welfare. The same tensions are a focus for work on group selection in evolution. To frame the matter simply, group selection would be expected to shape instincts fostering altruistic attitudes towards members of the same group, whereas individual level selection would

tend to develop the more selfish aspects of character. At an individual level, one would indeed expect selfish individuals to beat altruistic ones. But when it is possible to establish altruistic groups, they should, under certain conditions, out perform selfish groups. To quote Charles Darwin in a famous passage from 'The Descent of Man" :

"There can be no doubt that a tribe, including many members who were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection." [3]

Perhaps then the extent to which cooperation is favoured over defection in real human trials may reveal the influence of group selection in human evolutionary history. There are certainly those who advocate the importance of group selection in human evolution, see for example Sober and Wilson [43], or E. O Wilson quoted below,

"An unavoidable and perpetual war exists between honour, virtue and duty, the products of group selection on the one side, and selfishness, cowardice and hypocrisy, the products of individual selection on the other side...the human condition is an endemic turmoil rooted in the evolution process that created us. The worst in our nature coexists with the best, and so it will ever be." [5]

One might therefore claim that the contradictory pressures and opposing tensions of selection operating on multiple levels has fashioned mankind's ambivalent nature. It has made man enigmatic, ambiguous, difficult to understand. We have been forged in a compromise. It should come as no surprise that no one absolute tool or world view could comprehensively capture what it is to be human. Consciousness having evolved over millions of years, has been shaped by and for a long struggle for survival and reproduction. Conscious thought is driven largely by emotion, which frames and motivates thought. And emotion has been shaped by natural selection, perhaps even a subtle interplay of selection on several levels with contrary group and individual pressures. There is no reason a priori to believe that conscious thought should be amenable

to mathematical analysis or even to self examination. Following Colin McGinn, we might note that since the time of the Greeks mankind has made enormous progress in understanding the physical world, an area where mathematical understanding has borne fruit. But the problem of understanding subjective experience remains, with very little progress having been made in understanding since such questions were first framed in Greek times. Maybe therefore we should conclude that humans may never progress far in the study of their own minds.

To summarise so far, in terms of personal individual choice, the decision to cooperate in a Prisoners' Dilemma situation seems to be irrational. Nonetheless, this is what humans are biased to do. As Schelling comments:

"The premise of 'rational behaviour' is a potent one for the production of theory. Whether the resulting theory provides good or poor insight into actual behaviour is, I repeat, a matter for subsequent judgement". [10]

Classical game theory may be applicable to how computers might be expected to play one another. But human beings seem to be biased towards 'irrational' cooperative behaviour. But in being so biased human players may thereby accrue greater payoffs than their 'rational' counterparts. And therein lies a paradox that rational play may not be the optimal strategy, and one must be forced to anticipate the direction of the irrationality of ones opponent. Human decisions are not answerable to rationality alone, but must also conform to emotional pressures. Emotions are perhaps the principal mechanism by which natural selection has shaped human nature. Computers and artificial intelligence's on the other hand are not generally regarded as having feelings of any sort. One does not generally feel guilty at switching off ones computer, or replacing it with a newer, faster, more attractive model.

At the broader level of the social contract, one might conjecture that the collective decision to cooperate also has no rational basis, but that this has been cultivated by

natural selection acting at the group level. And the Prisoners' Dilemma then illustrates what is was intended to, which is that individual self interest can motivate actions that are contrary to the common good. The best response to any social dilemma is perhaps therefore to avoid it.

Broadening still further the concept of a social contract, one might think of a social contract problem for ants and bees, one that for the social insects has been solved by evolution. Indeed on might regard humans as being composed of a society of their tissues. The social contract type problem of stabilising cooperation may be seen to apply to the existence of multicellular life itself. Perhaps even to the society of DNA that comprises the chromosomes. One way to envisage cancer may be as the consequence of the breakdown of the social contract that regulates our internal tissues.

1.2 Game Theory and Evolution

In some sense, the application of game theory to the arena of biology and evolution seems to be more natural than its application to rational decision making. For example, we do not have to contend with the assumption of common rationality. Indeed, rationality is not invoked at all. In this case strategies are not adopted after conscious choice or a logical analysis of their likely consequences. Rather, a 'strategy' in evolutionary game theory is envisaged as a behavioural phenotype. It specifies the response of an individual to various situations. The payoff to each individual is to be interpreted as a contribution to its Darwinian fitness, a higher payoff leading to a larger number of offspring. The strategies that prevail in any given population will then be those that accrue the highest payoff scores and that therefore beget larger numbers to the next generation. Under the natural assumption that like should beget like, a strategy in this context is envisaged to be a heritable trait. Admittedly, in real systems, the link

between organism behaviour and genetics my be more complicated and is not well understood. This simplification of the relationship between behaviour and genetics has been termed the phenotypic gambit.

In 1981 Robert Axelrod invited submission of computer coded strategies to the Prisoners'Dilemma game. [18] Each strategy was then played against every other for 200 rounds. They were then ranked according to the payoff accumulated. Some strategies were quite complicated, but the overall winner was one of the very simplest, submitted by Anatol Rapoport, called TIT FOT TAT (TFT). This strategy plays Cooperate on the first move of a game, and thereafter it follows whatever choice was mad by its opponent in the previous round. A second competition was organised and TFT was again overall at the top of the accumulated payoff table. Axelrod identified some qualities of this strategy that seemed reasonably and intuitively to account for its success. Firstly, TFT was 'nice' in the sense that it would never be the first to defect. TFT was nonetheless 'provokable' in that it responded to an opponents defection by immediately defecting itself in the next round. TFT was also 'forgiving', in that it would cooperate with an opponent who cooperated in the previous round, despite its record of any previous defections. Axelrod provided a proof that TFT is an ESS in the Iterated Prisoners' Dilemma, provided that the number of iterations is sufficiently large. Thus TFT is an ESS for the Iterated Prisoners' Dilemma. So too, however, is the strategy 'Always Defect' (AD).

Reciprocal altruism has been observed in nature, most famously in the predator approach strategies of stickleback fish and the blood sharing behaviour of vampire bats [11]. Crucially, this requires the recognition of opponents.

Typically, the 'nasty' strategies in these tournaments do well for a while, gaining payoff scores from the more cooperative strategies. As a consequence, the number of nasty

strategies increases in the next generation. But soon they will begin to loose effectiveness as the prey they previously depended upon for their payoffs becomes more and more scarce. In their interactions with one another the nasty strategies do not do so well and consequently their numbers then begin to dwindle. Cooperators, on the other hand, tend to do rather well in the presence of other cooperators. These facts might suggest that it would be well to examine spatial effects in the interactions between cooperators and defectors. One might suspect that high concentrations of cooperators might thrive in areas that are on average depleted in the levels of defectors. It might also suggest that one investigate group selectionist pressures and examine how groups of cooperative individuals compete agains other less cooperative groups.

In 1964 John Maynard Smith proposed a simple model intended to show how group selection might operate to promote cooperation. [12] This is called the Haystack Model. The motivating tale runs as follows: in the autumn a farmer gathers his hay into stacks. These stacks are stored for the winter an then broken down for use once spring returns. These stacks are colonised by field mice for the winter. At winters end the mice flee the stacks and rejoin the field population. We allow two mice per stack. Over the winter these mice interact with one another via a Prisoners' Dilemma. The payoff received determines directly the number of progeny for each mouse. Mice reproduce asexually. If the mice remain confined for only one generation, then the situation is the same as in a well mixed randomly pairing population, and defectors out compete cooperators. However, if the mice are confined for multiple generations then the effect of their confinement is to ensure that subsequent to the first generation, there is a coordination in the strategies within each haystack. By the end of the winter, a haystack will either contain all cooperators or all defectors. Since cooperators do better when with other cooperators than to defectors with defectors, we may expect an increase in the number of cooperators produced. To give a specific example, consider the following Prisoners' Dilemma:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 2 & 0 \\ 3 & 1 \end{pmatrix} \end{array} \tag{1.1}$$

The above is the payoff matrix that governs the interaction if the mice within the haystack during the winter. In fact it gives the number of offspring for each mouse. Each mouse follows one or other of the strategies C (cooperate) or D (defect). The strategy of any particular mouse is fixed, and the same strategy is passed onto it progeny which are produced asexually. We consider that over the winter two rounds of the game are played, which is to say that the colonising mice play one round of the game. They reproduce according to their payoff and then die. Then their offspring play one round of the game with any other mouse that happens to be in the same stack. These mice then also reproduce according to their payoff and die, leaving the subsequent generation to prepare for the spring. Should a haystack initially be colonised by two defectors, then they will each receive payoff one. They then reproduce, each giving rise to a single defector. These then also interact to produce a third generation which prepare to flee. By the time spring arrives, two defecting mice are ready to emerge from this stack. A neighbouring stack may have been founded by one cooperator and one defector. When these mice interact, the defector receives payoff three and the cooperator payoff zero. Thus in the intermediate generation there are three defectors and no cooperators. The defectors then interact among themselves and (ignoring subtleties regarding paring), each gains payoff of one. There will therefore be three defecting mice ready to emerge from this stack at winters end. A final stack may have been colonised by two cooperators. When these play a round of the game with one another, each will receive a payoff of two, and therefore they will die and leave two offspring each. This intermediate generation of four cooperative individuals will also interact, each gaining payoff of two, so that by the time the stacks are torn down for the

spring, there will be eight cooperative mice ready to emerge from this haystack. In this way, the number of cooperative individuals may increase sufficiently to persist even in the midst others that defect. This is achieved by imposing a population structure that acts to coordinate the strategies that are played against one another. Since cooperators do so well when paired with other cooperators, such a coordination mechanism is to their advantage.

Another way to look at this scenario is to regard the goings on within the haystack, with its intermediate generations of mice, as a black box, and to focus instead on the situation as a game between the founders of the haystack colony. The different strategy combinations of the founders then ultimately give rise to different ensuing numbers of offspring. In our numerical example above, a defector founding a haystack colony with another defector can expect to obtain a single offspring at the end of the winter. So in this haystack game, the payoff to a defector against a defector will be unity. Likewise, when a cooperator founds a haystack with a defector, the cooperator will receive payoff zero and no progeny will result to him, whereas the defector can expect to bring forth three new defectors. Finally, when a haystack colony is founded by two cooperators, springtime should greet the emergence of eight new cooperators from their haystack. Which is to say that each founding cooperator gets payoff of four in the overall haystack game. Written in matrix form, the payoff matrix for this haystack game is:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 4 & 0 \\ 3 & 1 \end{pmatrix} \end{array} \tag{1.2}$$

This no longer has the structure of a Prisoners' Dilemma. This is in fact an example of the Stag Hunt game. The Stag Hunt can be thought of as a Prisoners' Dilemma with the

preference for payoffs R and T switched. It is regarded by some, such as Skryms [13] as a more appropriate model for social contract problems than the Prisoners' Dilemma.

1.3 Recent Background

The present work may be considered to overlap with the fields of evolutionary game theory as well as host-parasite systems and perhaps even disease dynamics.

Game theory as applied to evolutionary problems was first well formulated by Maynard Smith and Price [14], who in their paper formulated the first mathematical conditions for evolutionary stability of strategies. This work will be reviewed in the following chapter where we will outline the concept of an Evolutionary Stable Strategy (ESS).

A limitation of the ESS approach is that it is only capable of analysing consistently monomorphic populations. The evolution and stable states of a polymorphic population of strategists is accommodated by the work of Taylor and Jonker [15] and Zeeman [16] on what has become known as the replicator equation. This approached will also be outlined in the following chapter.

The replicator equation, being essentially a system of ordinary differential equations, does not explicitly take account of spatial effects. One notable analysis of spatial effects in game theory were the papers of Novak and May [21], [22], [23], [24], which examined a cellular automata model with interaction rules based on the payoff for the Prisoner's Dilemma. Some aspects of this work, including some simulation results, will be reviewed in Chapter Three.

Evolutionary game theory is one way of analysing frequency dependent fitness effects in evolution. Due to the complexity of biological phenomena, we should expect non linear effects to be of vital importance. A general review of non linear phenomena in

biology is well presented in [133]. An general overview of mechanisms for the evolution of cooperation is given in [106] in which is outlined direct reciprocity, indirect reciprocity, kin selection, group selection and network reciprocity (or graph selection).

As remarked above, the standard approaches to evolutionary game theory posit an infinite and well mixed population of players. In general one would expect that spatial aspects should be crucially important for biological and social systems. The infinite, continuous, well mixed populations that are treated in idealisations such as the replicator equation do not adequately reflect the complexity of the environment. After all, even at the level of common experience of economics, we can recognise that people occasionally pay high prices for goods because they may not be aware of the market rate which itself is because they do not live in a well mixed population. On the social level, some people commit crimes because they think there is a good chance that their actions will not be noticed by the authorities. This could not occur in a well mixed population in which case the police would be present at every point in space.

The assumption of a well mixed population is an idealisation that might apply for example in a well stirred flask of bacteria and nutrients. However in many natural settings we might expect spatial effects to have a profound impact on interactions. For example, in a well mixed scenario, the introduction of a pathogen into a population will be felt equally by all organisms in all locations. For a very small starting infection this would mean that each organism would be exposed to the same fractional level of infection. In real infection scenarios, one would expect firstly that the discreteness of the pathogen agents themselves should prevent this 'fractional exposure' situation. Taking space into account, one would also imagine that the exposure to a pathogen should vary considerably with location, with some organisms, by virtue of their distance from the source of infection, not feeling any immediate effect at all. Spatial approaches to ecological problems include the use of reaction diffusion equations [67], [68], [69] , [39] and metapopulation models in which space is represented as a set of

patches with no internal spatial structure [70], [71], [72]. An attempt to combine both approaches of reaction diffusion analysis with metapopulation set up is found for example in 'Stochastic spatial models' or 'interacting particle systems' and are discussed in [73]. Some of the findings reported in this paper are in accord with our own, namely that "Densities fluctuate wildly on small length scales, oscillate smoothly on moderate length scales, and after an initial transient are almost constant on large scales" [73].

In the language of infections and diseases, in well mixed populations, also known as mean field systems, all individuals have an equal likelihood of encountering infection, so the resulting strength of the infection in the population is the same for all [66]. Spatial heterogeneity and the local nature of interactions have been found to be crucially important considerations with regard to disease transmission and persistence, see for example [75], [76], [77], [54], [78]. Lattice models of infection have been given by [79], [74], [80]. The role of contact structures in such networks has been investigated extensively, see for example [81].

There are many ways in which spatial effects may be considered, and hence many reviews of the subject. A comparative study of different methods of treating spatial aspects in ecological models was made in [33]. The authors considered an interacting particle system as a formalism intended to represent essential features of patch models as well as the reaction diffusion approach. They noted that different spatial models can lead to different results and emphasized the importance of individuality (discreteness) in modelling biological systems. For a review of aspects of evolution in spatially structured populations, see [90] and [94] in which attention is confined to lattice models in which evolution proceeds by the imitation or colonisation mechanism. Both testify that within a certain parameter range, spatial lattice models can enhance success of comparative agents so that spatial considerations can outweigh the inherent advantage of defecting strategists. A review that is more ecologically centred is [100] and one focusing on microbial communities is [142].

The conventional non-spatial description of predator pray systems that also applies to host parasite systems is that of Lotka-Voltera. Further work along these lines that also neglects the effects of spatial structure can be found in [63], [64], [65]. One method of including the effects of space in epidemiological dynamics involves the use of reaction diffusion equations, [61], [62]. Studies have also been made of the spread of parasites in a spatially structured population, see for example [89] where the authors present results that differ from those of the conventional well mixed population approach. In particular they report that the transmission rate and virulence in a lattice structured population is significantly smaller than in a completely mixed population, and furthermore the spread of the parasite can drive the host to extinction, which is also in contrast to the completely mixed prediction.

The invasion of a host population by a pathogen has been studied on a lattice by various authors, see for example [60] who consider nearest neighbour transmission on a lattice. Those authors comment that "since the invasion of foreign organisms into the native or host population starts locally, spatial structures of the population need to be considered in order to study the ultimate success or failure of the invading species." The 'self shading' of parasites in a spatial model is described in [152], in which the parasite evolves to become less virulent than it would otherwize be in the case of global interactions.

Another simple spatial model of a genetic host-pathogen system is discussed in [74], and again the findings are in contrast to those of the mean field approach. In their model, which is a simple probabilistic cellular automata, lattice sites can be either empty or occupied by a single individual who may be either healthy or infected. This model is therefore somewhat insensitive to population density effects, in which for example a pathogen may reproduce in large numbers due to a large local concentration of hosts.

In the Prisoners' Dilemma, coexistence of pure strategy types (Always Defect and Always Cooperate) has been established for various spatial models. In [21], [22] it was demonstrated that over a wide range of parameters the simplest pure strategies of Always Cooperate and Always Defect persist indefinitely in coexistence. These results were extended to a random distribution of cells with a probabilistic factor introduced into the colonisation rule and were also extended to continuous time in [23] and [24]. The essential result is summarised in the last sentence of [23]: "..our overall conclusion is that interactions with local neighbours in two or three-dimensional spatial arrays can promote the coexistence of strategies, in situations where one strategy would exclude all others if the interactions occurred randomly and homogeneously." Our results presented below shall confirm this general expectation of the effect of space on game theoretic interactions. Coexistence in more general network models is discussed by many authors, see for example [58], [59].

A review of cellular automata models in game theory can be found in [111]. Extension to the Hawk-Dove game is discussed in [84]. A review of evolutionary graph theory that discusses game theory applications is [144].

The first cellular automata models of spatial game theory of [22], [21] can be regarded as having agents arranged at the vertices of a regular grid. A natural generalization of this approach is then to extend consideration to other network structures. This has given rise to the subject of evolutionary graph theory. An popular method of investigating spatial effects in game theory interactions has therefore been to analyse the effect of fixing players to a network or the vertices of a graph. Game theory played on a graph was introduced in [98] and has been been considered by numerous authors since. For a review that considers the effect of graph topology in the cases of Prisoners' Dilemma and Rock-Scissors-paper, see [136]. The point of view in evolutionary graph theory is that both well mixed populations and spatially structured ones can be modelled by

regular graphs upon which agents occupy the vertices and the network of contacts between them are the graph edges. Varied learned discourses have been written on the effect of graph topology on the effects of selection, the evolution of cooperation, and the coexistence of defecting and cooperating strategies in the Prisoners' Dilemma in particular, see [98], [58], [59] for examples.

In [83] the authors demonstrate for regular graphs, in the limit of weak selection, that cooperators and defectors may coexist. In such a scenario the fitness of an individual is given by $1-w+wP$, where P is the payoff from the game theory interaction and w is a number between zero and one that gives the strength of selection. For strong selection, $w=1$ and the individuals fitness is identical with its payoff P. For $w=0$ the fitness of an individual does not depend on the payoff at all. Thus the limit of weak selection is in a sense the limit in which the game theory interaction is becoming irrelevant to fitness and therefore to survival.

A phase diagram for the original cellular automata scenario of [21] has been given in [96], along with an extension to a complete 5-person game for the one shot Prisoners' Dilemma. An attempt to characterize the statistical properties of game theory cellular automata in terms of 'fundamental clusters' is given in [95]. The Prisoners' Dilemma on random graphs is investigated in [117]. The effect of changing the neighbourhood size is explored in [85]. Games on cycles are explored in [87]. The effects of the particular update rules used on the grid and the contribution of the payoff to reproduction is discussed in [113]. The effects of allowing the number of connections to change over time, for which there are various possible mechanisms, has been studied in [92], [109]. The effects of allowing a network to grow, and thereby also change the total population size, for which again there are presumably many possible mechanisms, are reported in [105] where the authors describe a 'payoff preferential attachment' Prisoners' Dilemma scenario. Whether growing networks further promote cooperation or defection turns out to be somewhat dependent on the game dynamics employed. The

Iterated Prisoners' Dilemma for the case of stochastic strategies with memory of one round is investigated on a lattice in [93] and the work offers further support to the already established notion that spatial structure enhances cooperative behaviour. In [104] a computational survey is made of several symmetric 2 X 2 games and different update rules on degree-homogeneous networks and thereby attempt to iron our some of the confusion in the literature regarding the conditions for coexistence. Myriad further refinements of games on grids are possible, for example [118] consider 'teaching rules' on a network for various social dilemmas that they claim "yields excessive benefits for the cooperators, substantially surpassing those that can be expected from spatiality alone". Or [119] consider a model where the strategy adoption rule is described by a parameter that is allowed to be selected for. The interaction between direct reciprocity and graph or network reciprocity is addressed in [108]. Analytical conditions for evolutionary stable strategies, which is to say conditions for a monomorphic population to be resistant to invasion by another strategy, have been considered for regular graphs of degree greater than two in [116]. The effect of allowing mutations in strategy on certain graphs is addressed in [110] where the authors derive analytical results for the limit of weak selection, in which as discussed above the game theory interaction is a marginal consideration for agent fitness.

Generally, explicit movement is not usually considered in such models, with strategies moving via imitation or the colonisation of neighbouring sites, usually at the end of each generation or time step.

The effects of spatial diffusion in a game theory context were perhaps first addressed in [121] in which agents were permitted to wander between patches without spatial structure. Diffusive dispersal of offspring was considered in [122], [123], [124], [125]. An explicit diffusive process in which a diffusive term was added to the replicator equation was given in [131], [132], though the game theory interactions still took place in a mean field fashion. A random walk on a lattice was investigated in [86] and [120] in

a Nowak and May type two dimensional stochastic cellular automaton model in which sites were allowed to be either occupied or vacant and in which diffusive movement was allowed to unoccupied sites in an agents immediate neighbourhood if any. A type of directed movement on a lattice has been proposed in [137]. A conditional mobility model on a lattice is described in [146] in the context of the Chicken Game.

Movement of a sort has been considered by [86] in which the authors consider simple pure strategy types where individual motion is governed by a non-contingent diffusive process. In their model, an agent may relocate to one of its four nearest neighbours provided that the chosen site is empty. Thus lattice sites are allowed to be empty, but they are not allowed to hold multiple agents. Thus agents can be prevented from moving if all adjacent lattice sites are already occupied. The authors found that for certain parameter regions, allowing this type of mobility could actually enhance the proportion of cooperators in the population. Movement on a lattice for the Prisoners' Dilemma and the Snowdrift and Stag Hunt games are considered in [120]. The effect of varying degrees of dispersal and neighbourhood size are considered in [143] in which it was reported that movement favours selfish individuals in both the Prisoners' Dilemma and the Snowdrift games and that spatial correlations should always be beneficial to cooperative strategies. A form of contingent motion has been studied in [88] in which cooperators move whenever they have experienced a defection in the previous round. In our model all agents move via a discetized diffusion process Different rates of host and pathogen movement are considered for example in [148].

Another way to enhance the level of cooperation in a population is to devise tags for agent strategy recognition. The effectiveness of cooperation can be greatly enhanced if there exists a system by which cooperators may reliably identify one another. However, any such recognition signal is also vulnerable to exploitation by cheaters [99].

As another example, recent work by Riole, Cohen and Axelrod [56] aims to demonstrate by means of computer simulations how cooperation may emerge in systems in which agents may identify others my means of a characteristic or tag and feel inclined to donate to those bearing the same tag. Although no memory of past encounters is now required, players are hear able to form a statistically reliable guess as to which of its game theory counterparts is likely to reciprocate. In this model counterparts are chosen form the population at random, thus the population is well mixed and spatial effects are not considered. We shall not consider the use of tags.

1.4 Thesis Outline

This thesis grew out of work to model the interaction between various types of parasitoid wasps and the insect larvae that incubate them. This was an individual based model based closely on the work of Scofield, Chaplain and Hubbard [25], [26]. The basic approach to the individual based model used has its origins in the work of Chaplain and Anderson [37], [38] on models of nematode movement and angiogenesis.

Many lines of code were written but this host-parasitoid model was never published. In thinking of a possible strategic or game theoretic summary for these host-parasitoid interactions, the thought occurred that it would be simpler and easier to code an individual based model in which the agents interacted directly via a game theory payoff matrix structure. I am not aware that this had been done before. The movement structure of agents responding to kairomone secretion was retained as a mechanism for allowing directed movement, though this background chemical field was sometimes set to zero and the agents then moved by a pure diffusion process.

The individual based model we consider in this thesis differs in significant respects to the majority of the network or graph theory cellular automata models referenced

above. In our model, it is possible for relatively unsuccessful strategies to persist in the environment as they are allowed to reproduce according to their accumulated payoff, not according to which strategy has locally scored the most. And explicit movement is also built into our model, so that several individuals, with differing strategies may occupy the same site. Mutation of strategies, in terms of the probabilities allocated in a mixed strategy, is also easily considered, as are non-synchronous generation dynamics.

Our work does not consider the weak selection limit in which so many analytical results have been obtained for other approaches. In the weak selection limit, one is actually assuming that the contribution of the game theory interaction to fitness is minimal. Indeed in the limit, the game theory payoff is irrelevant and one might therefore expect all strategies to coexist. In this thesis, the game theory payoff is the sole measure of reproductive fitness, and so in the appropriate terminology we might say that we are working in the 'strong selection' limit.

Our focus shall also be slightly different to the majority of work on the Prisoners' Dilemma in that we shall investigate the stability of an existing cooperating population when faced with the introduction of a single (mutant or foreign or invading) defector. We explore the stability of established cooperating populations when confronted with individuals following a defecting strategy. In this way our orientation is perhaps more towards a model of a host-parasite system rather than as a social model demonstrating the origin and durability of cooperation in the presence of defectors. In terms of the traditional concept of an Evolutionary Stable Strategy, we might comment that the most interesting and dynamic behaviour is observed when strategies coexist. In such cases it is possible for a small contingent of a differing strategy to invade a native population and establish itself as a stable proportion of the population. In this sense, the original native strategy cannot be said to be evolutionary stable, as it admits an invasion. Yet the invading contingent does not wholly supplant the native population.

Our approach differs from the cellular automata in further respects. Firstly we allow our agents to move. The movement rules being a random walk derived from an continuum limit diffusion equation. As a further elaboration, we also can allow a form of directed movement in the form of sensitivity to a chemical (kairomone) secretion. Also, in the cellular automata, each cell is occupied by a single player, and there are no voids containing no agents and no clusters or concentrations of agents. However, in our model, it is often the case that cells are empty, and there can be considerable expanses of vacant sites between concentrations of agents. Furthermore, we allow no limit to the number of agents occupying any one site. This aspect of allowing spatial clumpiness or crowding, rather than considering a uniform spatial distribution of agents as in a conventional network model, was felt to be integral to gaining a better understanding of the effects of spatial distribution that included the possibility of a local aggregations of agents. This approach to spatial populations therefore allows the possibility of local crowding or population depletion as a natural aspect of environmental inhomogeneity. Another aspect in which the present simulations might be considered to differ from the cellular automata work is perhaps in the clearer distinction between the individual and the strategy the individual employs. In the cellular automata set up, the individual that is tied to a particular cell will in the next time step adopt the strategy of those of his nearest neighbours that achieved the highest payoff in the previous round of the game. A different but consistent interpretation would be that the successful cell colonises other cells in the next time step. In network models there is thus a blurring of the concepts of imitation and colonisation or reproduction. In our model there is a much clearer distinction between individuals and strategies. Individuals persist for several timesteps and accrue a payoff over their lifetime that is translated directly into a number of offspring that then follow the same (genetically programmed) strategy. We do not require that agents compare their payoffs directly to decide who will survive or reproduce, rather the verdict on strategy viability is provided by the long term

accumulation in agent types. The effect of such differential reproduction may well be to the long term detriment of the less successful strategies, but this emerges from the simulation structure in a natural fashion, and is not input by hand as it seems to be in most network models. Thus even relatively unsuccessful individuals may be able to reproduce to be represented in the next generation, provided that hey have accumulated sufficient payoff. Also in our model mutual extinction is a possibility. We shall outline simulation parameter values for which the population of both strategies go to zero. Such mutual extinction could never happen in most cellular automata approaches, for in that case each cell must adopt some strategy. In the cellular automata model it is most natural to maintain a stable fixed population size, whereas in our model population is free to vary and find its own stable level. In a conventional cellular automata approach the population is constant. Not so in our model in which the population size is a natural and emergent property of the model structure.

Finally we shall allow the players to adopt mixed strategies, with a defined probability for defection for each agent. We allow this probability to mutate across generations and observe the resultant population profile of probabilities of defection. We find that the population generally evolves toward a high degree of defection, and this has a detrimental effect on the entire population level, and indeed as the population become almost pure defectors it heads toward extinction, [107]. This is reminiscent of some results in the host pathogen literature, in which it is found that pathogens evolve towards greater and greater virulence which often can force the host population to extinction. The metaphor in our case is not exact as the hosts and the pathogens in our example are actually the same thing, but the general notion of evolution to increased virulence and thereby extinction is loosely applicable.

Simulations were run for the most fashionable two player games, namely the Prisoners' Dilemma and the Hawk Dove game. The parameter space was scanned for regions

yielding interesting behaviour. Contrary to the mean field expectations, there were parameter regions in the Prisoners' Dilemma that exhibited sustained mutual coexistence of cooperators and defectors. However, the defectors were not able to survive without the cooperators. In this sense the motivation of the original host-parasitoid model remained, in that the natural interpretation of the defectors was as a parasite or infection within the cooperating population. Defectors were seen to regulate the cooperating population to a level much lower than the grid carrying capacity for cooperators in isolation. Both populations typically varied around stable long term average values. The behaviour was reminiscent of the regulation effect of parasites and infections in more complicated biological populations.

Chapter 2

A Brief Survey of Game Theory

2.1 Classical Game Theory

We consider only static games, also known as simultaneous decision games. In this case each player makes a single decision about what strategy to play. At the time the decision is to be made, a player will have no knowledge of what his opponent will choose to do. The payoff to each player will in general depend upon the choices made by both himself and his opponent.

We set out here the general notation for game theory. There will be a set of players, indexed by the integer $i \in \{1, 2, ...\}$. For each such player there will be a pure strategy set, denoted by $\mathbf{S}_i$. We also need to specify the payoff for each strategy combination. For two player games this is conventionally written as: $\pi_i(s_1, s_2)$ where $s_1 \in \mathbf{S}_1$ and $s_2 \in \mathbf{S}_2$. In translation, this expression reads: the payoff to player i when i plays strategy s_1 and his opponent plays strategy s_2. This notation is for two player games. We will not consider here games involving more than two players interacting at a single time.

In the general case, a player i may form his own strategy by selecting more than one pure strategy from the set $\mathbf{S}_i$. Such an agent may choose to play strategy $s_a \in \mathbf{S}_i$ with a fixed probability $p(s_a)$. Such a strategy is called a mixed strategy, and is denoted by σ_i. The set of all mixed strategies available to i is denoted by $\sum_i$.

We consider now the payoff to player i when he plays the mixed strategy σ_1 against an opponent that plays the mixed strategy σ_2. This can be written in terms of the pure strategies $s_1 \in \mathbf{S}_1$ and $s_2 \in \mathbf{S}_2$ and the probability $p(s)$ that i plays s and $q(s')$ that his opponent plays s':

$$\pi_i(\sigma_1, \sigma_2) = \sum_{s_1 \in \mathbf{S}_1} \sum_{s_2 \in \mathbf{S}_2} p(s_1) q(s_2) \pi_i(s_1, s_2) \tag{2.1}$$

Incidentally, since this equation represents a linear relationship, it may be cast in matrix form. We define the vector of probabilities $\mathbf{p} = (p(s_1), p(s_2), ..p(s_n))$ and write $\pi_i(s_j, s_k)$ as the matrix element $(\pi_i)_{jk}$ of π_i to give:

$$\pi_i(\sigma_1, \sigma_2) = \mathbf{p}^T . \pi_i . \mathbf{q} \tag{2.2}$$

The Nash Equilibrium

A solution in the context of game theory denotes an assignment of strategies to players which maximises the payoff to each under the assumption of rationality (CKR). A player cannot simply choose his highest payoff option, for he must take into consideration the actions of his opponent. The Nash equilibrium represents a stable solution for a game theory scenario, in that unilateral deviation from the prescribed equilibrium by a single player would not lead to him receiving a higher payoff score. A Nash equilibrium is called a strict Nash equilibrium if such unilateral deviation would definitely

lead to a lower payoff for the deviation player. Another way to express this is to say that, at the Nash equilibrium, each player has chosen the best response to the other players strategy. If we denote a pair of Nash equilibrium strategies by (σ_1^*, σ_2^*) then the Nash equilibrium condition can be written as:

$$\pi_1(\sigma_1^*, \sigma_2^*) \geq \pi_1(\sigma_1, \sigma_2^*) , \qquad \forall \sigma_1 \in \sum_1 \tag{2.3}$$

$$\pi_2(\sigma_1^*, \sigma_2^*) \geq \pi_2(\sigma_1^*, \sigma_2) , \qquad \forall \sigma_2 \in \sum_2 \tag{2.4}$$

There are many refinements concerning the existence of Nash equilibria in various circumstances and for different numbers of players. These will not concern us.

2.2 Evolutionary Game Theory

We consider a population of agents. Agents act in any given situation according to their assigned strategy. The strategy is considered to be essentially genetically programmed into the individual. John Maynard Smith termed such strategies 'behavioural phenotypes. Thus an agent cannot choose to alter the strategy followed, and an agents strategy is passed to its offspring.

In this thesis we consider only pairwise contest games, in which in each interaction, a given individual plays against a single opponent. In this case the payoff depends only upon the actions of the two agents towards one another. We do not consider games against the field, in which an individuals payoff is dependent on the composition of the entire population as a whole. Having said that, the composition of the general population is still important for it will determine the probability with which an individual

will encounter various other strategies.

In any given population there may be many individuals and many different strategies, either pure or mixed. On drawing a member of the population at random, there will be on average a probability $x(s)$ that the player one encounters will play the pure strategy $s \in \mathbf{S}$ in the following interaction.

We denote by $\mathbf{x}$ the vector of probabilities $x(s)$ with which each strategy $s \in \mathbf{S}$ occurs. This vector is termed the population profile and it denotes in some sense the average state of the population. We now consider what happens to a single individual that finds itself in such a population. Let this individual play a strategy denoted by σ. In one round of the game, the payoff to our particular individual will depend upon the strategy that is played by his opponent. This could be any member s of the set $\mathbf{S}$ for which $x(s)$ is non zero. This might depend, for example, on which particular opponent happened to be nearest to our individual at the time. If we consider an infinite, well mixed population, then the population profile $\mathbf{x}$ becomes a good approximation to the opposing strategy encountered by our individual. In this case we may write down the payoff to our individual in this population as:

$$\pi(\sigma,\mathbf{x}) = \sum_{s\in\mathbf{S}} p(s)\pi(s,\mathbf{x}) = \sum_{s\in\mathbf{S}}\sum_{s'\in\mathbf{S}} p(s)x(s')\pi(s,s') \tag{2.5}$$

Or in matrix form:

$$\pi(\sigma,\mathbf{x}) = \mathbf{p}^T.\pi.\mathbf{x} \tag{2.6}$$

Evolutionarily Stable Strategies

We aim to establish under what conditions a single strategy is resistant to invasion by some other strategy. We allow mixed strategies, so we aim to determine, given a population in which all players follow the same mixed strategy, whether it will be resistant to invasion. Consider a homogeneous population in which all players follow the same, possibly mixed, strategy σ^*. Into this population is introduced a small proportion ε of mutants or invaders which adopt a different strategy σ. After these mutants are introduced, the composition of the population will be changed. The new population is termed the post entry population, and the new population profile is written as $\mathbf{x}_\varepsilon$. If the payoff to the strategy σ^* in the post entry population, $\pi(\sigma^*, \mathbf{x}_\varepsilon)$, remains higher than the payoff to the mutants $\pi(\sigma, \mathbf{x}_\varepsilon)$, then the strategy σ^* is resistant to invasion and is said to be an Evolutionary Stable Strategy (conventionally abbreviated to ESS). The mathematical condition for this is written as:

$$\pi(\sigma^*, \mathbf{x}_\varepsilon) > \pi(\sigma, \mathbf{x}_\varepsilon) \tag{2.7}$$

Note that we have allowed the ESS σ^* to be a mixed strategy. Therefore we should consider what happens when a population that follows this ESS strategy encounters a player that is following one of the component pure strategies of the ESS. Let $\mathbf{x}^*$ be the population profile generated by the strategy σ^*. We denote the set of pure strategies which compose σ^* by $\mathbf{S}^*$ and call this the support of σ^*. If the population is to be stable then we will require that:

$$\pi(s, \mathbf{x}^*) = \pi(\sigma^*, \mathbf{x}^*) \quad \forall s \in \mathbf{S}^* \tag{2.8}$$

Proof: If the above is not true, then some strategies in the support of σ^* must give a

lower payoff and some a higher payoff. Let s' be one such strategy that gives a greater payoff. Then we can write:

$$\pi(\sigma^*, \mathbf{x}^*) = \sum_{s \in \mathbf{S}^*} p^*(s)\pi(s, \mathbf{x}^*) \tag{2.9}$$

$$= \sum_{s \neq s'} p^*(s)\pi(s, \mathbf{x}^*) + p^*(s')\pi(s', \mathbf{x}^*) \tag{2.10}$$

$$< \sum_{s \neq s'} p^*(s)\pi(s', \mathbf{x}^*) + p^*(s')\pi(s', \mathbf{x}^*) \tag{2.11}$$

$$= \pi(s', \mathbf{x}^*) \tag{2.12}$$

Which establishes the result by contradiction. We can understand this result intuitively by considering two strategies, s_a and s_b in the support of σ^*. If it was the case that $\pi(s_a, \mathbf{x}^*) > \pi(s_b, \mathbf{x}^*)$ then it would seem reasonable to adopt s_a more often that s_b. But then σ^* would no longer be an ESS.

Thus although we have established that a monomorphic population in which everyone plays the strategy σ^* is evolutionary stable, it also seems that, in this population, individuals using strategies in the support of σ^* accrue the same payoff, and therefore have the same fitness as those using σ^* itself. However, none of these pure strategies is necessarily an ESS in its own right, (for that would require that $\pi(s, \mathbf{s}_\varepsilon) > \pi(\sigma, \mathbf{s}_\varepsilon)$ and this is by no means follows from what has been written above). It remains here an open question whether a population of individuals each pursuing pure strategies, with those strategies occurring in the same proportions as the probabilities $p(s)$ in the definition of the ESS strategy σ^*, would also be resistant to invasion. It would seem reasonable

that this be so, as the population profile **x** is the same in both cases. However, in this situation, as there is not a single strategy followed each member of the population, it would be inappropriate to apply the conditions for an ESS directly. Rather we should consider the issue of whether a population so constituted would be resistant to invasion and therefore in an evolutionary stable state. We will address this case below in the section on the Replicator Equation.

The ESS and Nash Equilibria

As noted above, in a pairwise contest population game the payoff to an individual playing σ in a population with profile **x** is:

$$\pi(\sigma, \mathbf{x}) = \sum_{s \in \mathbf{S}} \sum_{s' \in \mathbf{S}} p(s)x(s')\pi(s, s') \tag{2.13}$$

This payoff is the same as would be achieved in a two player game against an opponent using a strategy σ' that assigns probabilities $p'(s) = x(s) \forall s \in \mathbf{S}$. Thus we can always associate a two player game with a population game involving pairwise contests.

Consider a pairwise contest and let σ^* be an ESS. We shall show that $\forall \sigma \neq \sigma^*$ one of the following obtains:

$$\pi(\sigma^*, \sigma^*) > \pi(\sigma, \sigma^*), \ or \tag{2.14}$$

$$\pi(\sigma^*, \sigma^*) = \pi(\sigma, \sigma^*) \ and \ \pi(\sigma^*, \sigma) > \pi(\sigma, \sigma) \tag{2.15}$$

These conditions were first given by Marynard Smith and Price in 1973. [14] Any strategy that satisfies these conditions in a pairwise contest is an ESS.

Proof: since σ^* is an ESS, we may write:

$$\pi(\sigma^*, \mathbf{x}_\varepsilon) > \pi(\sigma, \mathbf{x}_\varepsilon) \tag{2.16}$$

Where the post entry population is given by $\mathbf{x}_\varepsilon = (1-\varepsilon)\sigma^* + \varepsilon\sigma$, which is to say that a proportion ε of the population plays strategy σ and the remaining $(1-\varepsilon)$ play σ^*. Using the linearity of the payoff function π we can write the left hand side as:

$$\pi(\sigma^*, \mathbf{x}_\varepsilon) = \pi(\sigma^*, (1-\varepsilon)\sigma^* + \varepsilon\sigma) = (1-\varepsilon)\pi(\sigma^*, \sigma^*) + \varepsilon\pi(\sigma^*, \sigma) \tag{2.17}$$

and the right hand side can similarly be written as:

$$\pi(\sigma, (1-\varepsilon)\sigma^* + \varepsilon\sigma) = (1-\varepsilon)\pi(\sigma, \sigma^*) + \varepsilon\pi(\sigma, \sigma) \tag{2.18}$$

combining these equations then gives:

$$(1-\varepsilon)\pi(\sigma^*, \sigma^*) + \varepsilon\pi(\sigma^*, \sigma) > (1-\varepsilon)\pi(\sigma, \sigma^*) + \varepsilon\pi(\sigma, \sigma) \tag{2.19}$$

Since we assume that ε is much smaller than unity, the required result follows.

These conditions enable us to identify an ESS in a pairwise contest population game by finding the symmetric Nash equilibria of the associated two player game, and then testing these equilibria under the ESS conditions above.

The Replicator Equation

This approach, in contrast the the ESS approach above, aims to determine what will happen to a population of diverse individuals, in which several different strategies are allowed to compete and coexist. We consider again individuals that adopt only pre-programmed strategies (behavioural phenotypes), and that such strategies are inherited without modification by its descendants. Unlike in the discussion of the ESS, we allow there to be several different behavioural phenotypes. Also unlike the ESS case, we do not allow mixed strategies to occur, individuals are only permitted to adopt pure strategies. We denote the pure strategy set by $\mathbf{S} = \{s_1, s_2, ..., s_k\}$. Let n_i be the number of players that use pure strategy s_i. The total population size is:

$$N = \sum_{i=1}^{k} n_i \tag{2.20}$$

The frequency of s_i strategists in the population is:

$$x_i = \frac{n_i}{N} \tag{2.21}$$

The state of the population can then be represented by the vector:

$$\mathbf{x} = (x_1, x_2, ..., x_k) \tag{2.22}$$

We denote the per capita birth and death rates by β and δ respectively. Consider a s_i strategist in a population in state $\mathbf{x}$. On average, the payoff to this player in a single round of that game will be $\pi(s_i, \mathbf{x})$. If we assume that this payoff value contributes in the simplest way to the growth rate of the n_i population, as do the fixed birth and death rates, then we may write:

$$\frac{dn_i}{dt} = (\beta - \delta + \pi(s_i, \mathbf{x}))n_i \tag{2.23}$$

And the overall population size will comprise the sum of all these as:

$$\frac{dN}{dt} = \sum_{i=1}^{k} \frac{dn_i}{dt} \tag{2.24}$$

$$= \sum_{i=1}^{k} (\beta - \delta + \pi(s_i, \mathbf{x}))n_i \tag{2.25}$$

$$= (\beta - \delta) \sum_{i=1}^{k} n_i + \sum_{i=1}^{k} \pi(s_i, \mathbf{x})n_i \tag{2.26}$$

$$= (\beta - \delta)N + N \sum_{i=1}^{k} x_i \pi(s_i, \mathbf{x}) \tag{2.27}$$

$$= (\beta - \delta + \bar{\pi}(\mathbf{x}))N \tag{2.28}$$

Where we have introduced the average payoff to a player in the population as:

$$\bar{\pi}(\mathbf{x}) = \sum_{i=1}^{k} x_i \pi(s_i, \mathbf{x}) \tag{2.29}$$

Our aim here is to determine the composition of the population and which strategies will be successful We will therefore attempt to factor out the overall size of the population N. Since:

$$\frac{dn_i}{dt} = N\frac{dx_i}{dt} + x_i\frac{dN}{dt} \tag{2.30}$$

We may write:

$$N\frac{dx_i}{dt} = \frac{dn_i}{dt} - x_i\frac{dN}{dt} \tag{2.31}$$

$$= (\beta - \delta + \pi(s_i, \mathbf{x})x_i N - x_i(\beta - \delta + \bar{\pi}(\mathbf{x}))N \tag{2.32}$$

Cancelling the common factor of the population size N yields:

$$\frac{dx_i}{dt} = (\pi(s_i, \mathbf{x}) - \bar{\pi}(\mathbf{x}))x_i \tag{2.33}$$

This expresses the perhaps intuitively obvious conclusion that a strategy will increase in proportion if it receives a payoff higher than the average, and conversely a strategy that receives a payoff lower than the population average will decline in proportion.

A population is stable when the values of x_i are constant. In this case the population is no longer evolving. Mathematically we have $\frac{dx_i}{dt} = 0$, which is to say a fixed point of the above differential equation.

When there are only two strategies available then the equations admit of a further simplification. Let the strategy set be $\mathbf{S} = \{s_1, s_2\}$. We define $x = x_1$. Since by definition we have $x_1 + x_2 = 1$, we may write $x_2 = 1 - x$ and $\frac{dx_2}{dt} = -\frac{dx_1}{dt} = -\frac{dx}{dt}$.

As we may easily calculate x_2 from x_1 via the equation $x_1 + x_2 = 1$, we need only consider the differential equation for x_1:

$$\frac{dx}{dt} = (\pi(s_1, \mathbf{x}) - \bar{\pi}(\mathbf{x}))x \tag{2.34}$$

We can further simplify this to remove the averaged payoff by substituting in

$$\bar{\pi}(\mathbf{x}) = x\pi(s_1, \mathbf{x}) + (1-x)\pi(s_2, \mathbf{x}) \tag{2.35}$$

to give:

$$\frac{dx}{dt} = x(1-x)(\pi(s_1, \mathbf{x}) - \pi(s_2, \mathbf{x})) \tag{2.36}$$

The equilibria for this ODE are given by the solutions to the equation $\frac{dx}{dt} = 0$. These solutions are therefore the fixation points, $x = 0$ and $x = 1$ as well as all points that satisfy the equation $\pi(s_1, \mathbf{x}) - \pi(s_2, \mathbf{x}) = 0$. The equilibrium at $x = 0$ is stable if $\pi(s_1, 0) < \pi(s_2, 0)$. The equilibrium at $x = 1$ is stable for $\pi(s_1, 1) > \pi(s_2, 1)$. Any non trivial equilibrium points, x^*, will be stable provided that $\frac{d\pi(s_1,x)}{dx} < \frac{d\pi(s_2,x)}{dx}$ when evaluated at $x = x^*$. From these results it can be shown that every symmetric Nash equilibrium corresponds to a fixed point in the replicator dynamics, although not every fixed point will correspond to a Nash equilibrium.

We shall now apply these results to the main games considered in this thesis.

2.3 The Hawk Dove Game

This game was considered by Maynard Smith and Price in their landmark paper that developed the field of evolutionary game theory. This game was considered as a model of within species conflicts. Previously it had been held that it was for the good of

the species that conventional intra species competition, in which outcomes are decided by display or otherwise, usually operated without recourse to deadly force. Maynard Smith sought to counter this group selectionist argument, and offered an analysis of the Hawk Dove game to demonstrate that two different conflict strategies might coexist in a single population.

In this game there are two pure strategies, Hawk H and Dove D. Players contest a resource of value V. Should two Hawks meet, then each has an equal chance of obtaining the resource V or of being injured and incurring a fitness cost of C. Thus in Hawk-Hawk contests, a given player will successful half of the time. Therefore, on average, the payoff to a Hawk in a Hawk-Hawk contest will be $\frac{1}{2}(V-C)$. When a Hawk encounters a Dove, the Hawk will obtain the resource and the Dove will retreat directly. Thus in a Hawk-Dove encounter, the payoff to the Hawk will be V and the Dove will receive zero payoff. In Dove-Dove contests, the resource is shared equally between the contestants. Thus each receives payoff $\frac{V}{2}$. The payoff matrix is therefore given by:

$$\begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} \frac{1}{2}(V-C) & V \\ 0 & \frac{V}{2} \end{pmatrix} \end{array} \tag{2.37}$$

Nash Equilibria

It turns out that there are two distinct regimes for this game, related to value of the resource V compared to the cost of injury C. In general if the value of the resource is higher than the cost of injury, then the dominant strategy is clearly to play as a Hawk. However, when the cost of injury exceeds the resource value then a mixed strategy is favoured.

Case $V > C$

For the case $V > C$ it is clear that the pure strategy Hawk is the best response to Hawk. Thus to play Hawk is in this case a Nash equilibrium.

Case $V < C$

For the case $V < C$ there is no pure strategy Nash equilibrium, and we need to examine the possibility of a mixed strategy Nash equilibrium which we denote by σ^*. We proceed by using the fact that, for a mixed Nash equilibrium, the payoff to any strategy in the support of the equilibrium is equal to the payoff to the Nash equilibrium strategy itself. Let the Nash equilibrium be a mixed strategy that plays H with probability q and plays D with probability $1-q$. Therefore for player one we may write:

$$\pi_1(H,\sigma^*) = \pi(D,\sigma^*) \tag{2.38}$$

$$\begin{pmatrix} 1 & 0 \end{pmatrix} \cdot \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \cdot \begin{pmatrix} q \\ 1-q \end{pmatrix} = \begin{pmatrix} 0 & 1 \end{pmatrix} \cdot \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \cdot \begin{pmatrix} q \\ 1-q \end{pmatrix} \tag{2.39}$$

$$q\frac{V-C}{2} + (1-q)V = (1-q)\frac{V}{2} \tag{2.40}$$

$$q = \frac{V}{C} \tag{2.41}$$

Likewise for player two. Thus the Nash equilibrium is for each player to adopt a mixed strategy, playing H with probability $\frac{V}{C}$:

$$\sigma^* = \begin{pmatrix} \frac{V}{C} & 1 - \frac{V}{C} \end{pmatrix} \tag{2.42}$$

Evolutionary Stable Strategies

Case $V > C$

For the case $\frac{V-C}{2} > 0$, or $V > C$, the strategy H is an ESS. Again this can be rationalised as regarding it always being worth the cost of injury for the chance to obtain a resource of greater value. Thus in this regime, a population of Hawks should be resistant to invasion by Doves.

Case $V < C$

In this case there is no pure strategy ESS. Clearly H is not an ESS in this case, and neither is D since $\pi(D,D) < \pi(H,D)$. We will now show that the above Nash equilibrium is also an ESS for the corresponding population game. To do this we show that one of the conditions 2.14 or 2.15 holds for all $\sigma \neq \sigma^*$. As σ^* is a mixed strategy, we have $\pi(\sigma^*,\sigma^*) = \pi(\sigma,\sigma^*)$, which means the condition 2.14 is not satisfied. Thus we need to check that the second ESS condition is obeyed, i.e that the ESS strategy σ^* does better agains the invading strategy σ that the invading strategy does against itself. We let the strategy σ^* play H with probability q, as we did above, and assume the strategy σ plays H with probability p.

$$\pi(\sigma^*,\sigma) > \pi(\sigma,\sigma) \tag{2.43}$$

$$\begin{pmatrix} q & 1-q \end{pmatrix} \cdot \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \cdot \begin{pmatrix} p \\ 1-p \end{pmatrix} > \begin{pmatrix} p & 1-p \end{pmatrix} \cdot \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \cdot \begin{pmatrix} p \\ 1-p \end{pmatrix} \tag{2.44}$$

$$qp\frac{V-C}{2} + qV(1-p) + (1-q)(1-p)\frac{V}{2} > p^2\frac{V-C}{2} + Vp(1-p) + (1-p)^2\frac{V}{2} \tag{2.45}$$

This can be re-arranged as:

$$p\frac{V-C}{2}(q-p) + V(1-p)(1-q) + \frac{V}{2}(1-p)(p-q) > 0 \tag{2.46}$$

which can be simplified to:

$$(q-p)^2\frac{C}{2} > 0 \tag{2.47}$$

Since $C > 0$, and $q \neq p$, this inequality certainly holds. Therefore the ESS for the Hawk Dove game is σ^*, which is a mixed strategy playing H with probability $\frac{V}{C}$, the same as the Nash equilibrium for the corresponding two player game.

Replicator Dynamics

Case $V < C$

In the above section, the ESS was shown to be a mixed strategy, namely to play H with probability $\frac{V}{C}$. We now examine whether the corresponding proportions of pure strategies in a population makes for an evolutionary stable state. We denote the proportion

of H players in the population by x. Into equation 2.36 we substitute the strategies H for s_1 and D for s_2 and recall that in this case we can write the population profile as $\mathbf{x} = xH + (1-x)D$.

$$\pi(s_1, \mathbf{x}) - \pi(s_2, \mathbf{x}) = \pi(H, \mathbf{x}) - \pi(D, \mathbf{x}) \tag{2.48}$$

$$\begin{pmatrix} 1 & 0 \end{pmatrix} \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix} - \begin{pmatrix} 0 & 1 \end{pmatrix} \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix} \tag{2.49}$$

$$= x\frac{V-C}{2} + V(1-x) - \frac{V}{2}(1-x) \tag{2.50}$$

$$= \frac{V}{2} - \frac{xC}{2} \tag{2.51}$$

Therefore the replicator equation in this instance becomes:

$$\frac{dx}{dt} = \frac{C}{2}x(1-x)\left(\frac{V}{C} - x\right) \tag{2.52}$$

We may identify the fixed points x^* directly as $x^* = 0$, $x^* = 1$ and $x^* = \frac{V}{C}$. If $x < \frac{V}{C}$ then $\frac{dx}{dt} > 0$ and the fixed point at zero is unstable. If $x > \frac{V}{C}$ then $\frac{dx}{dt} < 0$ and the fixed point at $x = 1$ is unstable. Thus for any initial configuration of the population that is not a fixed point, we have $x \to \frac{V}{C}$.

This is the mixed polymorphic population counterpart of the ESS result for a single mixed strategy population. It states that a population with proportion $\frac{V}{C}$ that plays Hawk and the remainder playing Dove, is in an evolutionary stable state.

Case $V > C$

In this case we have $\frac{V}{C} - x > 0$ and so $\frac{dx}{dt} > 0$ for $x \neq 0$, $x \neq 1$. Thus a population that contains at least some Hawks will evolve towards the fixed point at which the entire population are Hawk players.

Discussion

The Hawk Dove game was one of the first to be considered in Evolutionary Game Theory. The motivation for Maynard Smith to discuss this example was in part to counter certain group selectionist arguments. In many species, individuals frequently come into conflict regarding all sorts of things, such as mating sites and territories, and food sources. Often times these individuals may have rather lethal fighting attributes, such as horns or sharp teeth or poisonous stings. Since it is always better to have a resource than to not have it, conflict seems inevitable. The issue then becomes, why do animals not utilise the full force of all their deadly attributes to settle such conflicts, fighting to the death if necessary? In the past, a conventional argument was that such mortal conflict would be contrary to the good of the species, and therefore natural selection has selected for survival only those species whose individuals do not mortally contest one another. This seems superficially plausible, and as remarked in the introduction, Darwin himself wrote of the possibility of group selection. However, at the individual level there would surely remain the opportunity for some individuals to break with the convention and contest resources more aggressively. Such animals would likely gain a greater share of resources then they would if following the non-aggressive convention. These individuals would then be expected to foster more offspring and therefore become a greater proportion of the population. After several generations the proportion of aggressive individuals will have increased so much that, in the end, the best course

of action for all would be to fight doggedly in every contest. Thus it might seem that such 'for the good of the species' arguments were open to objection. Some biologists, including Maynard Smith in particular, were uneasy with explanations that overlooked competition at the individual level. In devising Evolutionary game theory and the Hawk-Dove game, Maynard Smith wished to illustrate how a range of strategies for conflict might exist in a population with selection operating only at the individual level.

2.4 The Prisoners' Dilemma

The Prisoners' Dilemma was introduced to game theory in 1950 by two RAND corporation scientists, Merril Flood and Melvin Dresher. In May the same year, Albert Tucker presented a lecture to the psychology department of Stanford University in which he coined the name "Prisoners' Dilemma" and provided what has become since the convention background motivating story. This story is as follows: two criminals are held by police for questioning. They are detained in separate cells and cannot communicate with one another. The police attempt to persuade the criminals to confess, knowing that without a confession there is only sufficient evidence to convict on a minor charge. The police therefore make the same offer to each prisoner individually: If one of them confesses and one does not, then the confessor will be set free and the other will receive the maximum sentence possible, say ten years. However, if both confess then each will face the same prison sentence of seven years. If neither confesses then the lesser offence will carry a lower penalty for both, say two years. The question is, what is the logical thing to do in this predicament? In discussions of the Prisoners' Dilemma, action "not confess" is usually termed "cooperation" (which is to say cooperation with one's fellow criminal in the motivating example story), and the action "confess" is labelled "defect" (i.e. betraying one's associate in this example). We shall denote these two strategies by C for cooperate and D for defect.

In matrix form this particular instance of the Prisoners' Dilemma takes the form:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} -2 & -10 \\ 0 & -7 \end{pmatrix} \end{array} \tag{2.53}$$

Consider the possible actions available to player 1; should player 2 keep quiet, then player 1 has the choice between keeping quiet (cooperating) and receiving a payoff of -2 or confessing (defecting) for a payoff of 0. Assuming that the payoff matrix represents a true reflection of the players preferences, the rational choice is to maximise one's payoff and therefore player 1 should choose to confess (defect). However, if player 2 were to confess (defect), then the best option for player 1 would also be to defect, for this entails a payoff of -7 as opposed to a payoff of -10 were player 1 to choose not to confess (cooperate). In each case, the choice for player 1 that maximises his payoff is the strategy 'defect'. As the game is symmetric, the same conclusion applies to player 2.

The general form of a Prisoners' Dilemma payoff matrix is given by:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{2.54}$$

with $T > R > P > S$, where conventionally one calls T the temptation to defect, R the reward for cooperation, P is the punishment for mutual defection and S is the suckers payoff to a cooperator against a defector.

Nash Equilibrium

In a Prisoners' Dilemma situation, the strategy Defect D is clearly the best response to itself. Therefore Defect is the Nash equilibrium strategy for this game.

Evolutionary Stable Strategies

If each player has no memory of the result of previous interactions, which is to say if the strategy set is restricted to any mixed strategy formed from the two pure strategies Defect D and Cooperate C, then the only ESS is Defect.

Replicator Dynamics

We consider a game based on the payoff matrix 2.67. We substitute this payoff structure into the replicator equation 2.36. We let s_1 be the strategy C and s_2 be D and x be the proportion of C players in the population. Thus we have:

$$\pi(s_1,\mathbf{x}) = \pi(C,\mathbf{x}) = \begin{pmatrix} 1 & 0 \end{pmatrix} \begin{pmatrix} R & S \\ T & P \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix} = Rx + S(1-x) \tag{2.55}$$

Likewise we also have:

$$\pi(s_2,\mathbf{x}) = \pi(D,\mathbf{x}) = \begin{pmatrix} 0 & 1 \end{pmatrix} \begin{pmatrix} R & S \\ T & P \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix} = Tx + P(1-x) \tag{2.56}$$

substituting into the replicator equation 2.36 gives:

$$\frac{dx}{dt} = x(1-x)\Big((R+P-S-T)x+S-P\Big) \tag{2.57}$$

The fixed points for this system are located at $x = 0$ and $x = 1$.

Using the relation that defines the Prisoners' Dilemma payoff $T > R > P > S$ we have $R+P-S-T < T+P-S-T$, we may write:

$$\frac{dx}{dt} < x(1-x)\Big((P-S)x-(P-S)\Big) \tag{2.58}$$

$$\frac{dx}{dt} < x(1-x)(S-P)(1-x) \tag{2.59}$$

Since $P > S$ we have $S-P < 0$. With this in mind, for $x \in (0,1)$, the above becomes:

$$\frac{dx}{dt} < 0 \tag{2.60}$$

Drawing all these results together, we note that for any population that does not start at a fixed point of the dynamics, since $\frac{dx}{dt} < 0$, the population will evolve towards the state $x = 0$, which is the Nash equilibrium in which all play the strategy Defect D.

2.5 Rock, Paper, Scissors

This is a two player game with three strategies, frequently played by children. The players make a simultaneous choice between the options of Rock R, Paper P and Scissors S, with Rock beating Scissors, Scissors beating Paper and Paper beating Rock.

Conventionally if both players select the same item then the result is a draw and usually they will play again. The payoff matrix for this game is as follows:

$$\begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix} \end{array} \tag{2.61}$$

There is an alternative version of the game in which a small payment $\varepsilon > 0$ is made in the event of a draw. in this case the payoff matrix becomes:

$$\begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{pmatrix} -\varepsilon & 1 & -1 \\ -1 & -\varepsilon & 1 \\ 1 & -1 & -\varepsilon \end{pmatrix} \end{array} \tag{2.62}$$

Nash Equilibrium

There is a unique Nash equilibrium for both versions of the game,which is the mixed strategy $\sigma^* = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$.

Evolutionary Stable Strategies

A game with only two pure strategies will always have at least one ESS [cite maymard smith]. This is no longer the case in three strategy games. The pure form of the Rock Scissors Paper game does not have an ESS because:

$$\pi(\sigma^*, R) = 0 = \pi(R, R) \tag{2.63}$$

The alternative version has an ESS which is the same as the Nash equilibrium: $\sigma^* = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$.

Replicator Dynamics

We consider the pure form of the game. Writing the respective proportions of R, S and P players by x_R, x_S and x_P, the replicator equations become:

$$\frac{dx_R}{dt} = x_R(x_S - x_P) \tag{2.64}$$

$$\frac{dx_S}{dt} = x_S(x_P - x_R) \tag{2.65}$$

$$\frac{dx_P}{dt} = x_P(x_R - x_S) \tag{2.66}$$

The fixed points are $(1,0,0)$, $(0,1,0)$, $(0,0,1)$, and $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$. The first three are not stable, the last can be shown to be of neutral stability, so that there can be oscillatory behaviour around this fixed point.

For the alternative version of this game, the genetically polymorphic population $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is unstable.

2.6 The Stag Hunt

The origins of this two player game go back to a very short passage in Rousseau's Discourse on Inequality. In the motivating tale, there are two hunters. They have the choice to hunt either hare or stag. A stag is much more valuable than a hare, but there is no chance that a single individual can bring down a stag. To successfully hunt stag therefore requires coordination, or cooperation. A hare on the other hand can be caught by an unaided individual. The Stag Hunt is another social dilemma game, related to the Prisoners' Dilemma in that the preferences of the reward R and temptation T payoffs are switched. Thus the payoff matrix for a generic Stag Hunt is written as:

$$\begin{array}{c} \\ S \\ H \end{array} \begin{array}{c} \begin{array}{cc} S & H \end{array} \\ \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{2.67}$$

where S represents the strategy of hunting stag, and H that of hunting hare and where $R > T > P \geq S$.

Both stag hunting and hare hunting are Nash equilibria in this game. The Stag Hunt differs from the Prisoners' Dilemma in that what one player decides to do will depend on what his beliefs are about the other players choice. Choosing to hunt stag is however risky, in that if ones opponent chooses to hunt hare then the stag hunters payoff will be low. But a hare hunter runs no such risk, as the payoff to hare hunting is independent of the choice of the other player. In the Stag Hunt, cooperation is an equilibrium state, unlike in the Prisoners' Dilemma. The tension then becomes one between considerations of mutual benefit and personal risk. The Stag Hunt is regarded by some [7] as a more realistic encapsulation of the problem of establishing some form of social contract. In some sense this seems to be a reasonable view, given that one

would expect any resulting social contract to be a stable equilibrium state.

As related in chapter one, the Stag Hunt can be seen as an outcome of a repeated Prisoners' Dilemma. This therefore indicates that there is a mechanism to stabilise cooperation once cooperation is established. But the problem of how to establish co-operation is still open. The Stag Hunt does not solve the problem of cooperation, but it allows cooperation as an equilibrium state.

Chapter 3

Game Theory With Cellular Automata

In this chapter we reproduce some of the results to one of the most notable explorations of spatial game theory, as reported by Novak and May. [21], [22] We consider a grid in which each site is populated by a single player. In each timestep a player will engage in a single round with each of its nearest neighbours. We consider only the case in which an interior grid point to have eight nearest neighbours, with the number of neighbours correspondingly reduced the boundary grid points. At the end of each timestep for all cells we compare the payoff received by a that cell and each of its nearest neighbours. For the next round this central cell will then adopt the strategy of that cell among its neighbours that scored the highest payoff. In this way, each cell will imitate what in the last time step was locally observed to be the most lucrative strategy. We consider only the two basic pure and unconditional strategies for the prisoners Dilemma, namely Always Defect (AD) and Always Cooperate (AC). As such there is no stochastic aspect to these simulations and the results that follow are the result of purely deterministic processes. A notable feature of these simulations is firstly the character of the spatial patterns exhibited, which have been described as dynamic fractals. Also important is the result that , for a certain parameter range, the two strategies AC and AD persist

indefinitely in fluctuating proportions about stable long term average values. This is similar to the results claimed in the main part of this thesis. It is important to note that no sophisticated strategies are here required to stabilise the existence of cooperative strategies in a population in which defectors are also present. Indeed, no memory is required at all. This work demonstrates that spatial considerations can allow outcomes that are counterintuitive and that differ from the naive perspective of classical game theory, and evolutionary game theory that usually assumes well mixed populations.

3.1 Outline of the Model

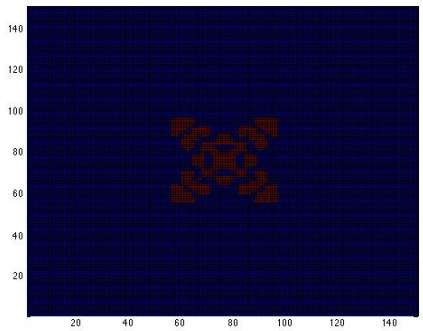
We consider an n by n grid. Cells in the interior of the grid have eight nearest neighbours, those on the edge have correspondingly fewer neighbouring cells. We do not consider grids with edges identified by periodic or anti periodic boundary conditions, in the manner of a cylinder, torus, projective plane or a Klein Bottle, though these would be easy enough to code for. The payoffs for the Prisoner's Dilemma are set to be $R = 1$, $T = b$ where $b > 1$, and $S = P = 0$. In matrix form we have:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 1 & 0 \\ b & 0 \end{pmatrix} \end{array} \tag{3.1}$$

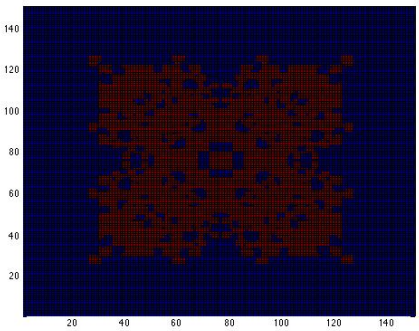
Thus the payoff due to a pair of defectors is the same as that due to a cooperator when encountering a defector, each being zero. The payoff to each in a pair of cooperators is unity, and a defector scores b agains a cooperator (which would then have payoff zero). Thus the parameter b reflects the advantage of defectors over cooperators. In this set up, the only parameter that we shall vary will be b.

3.2 Simulation Results

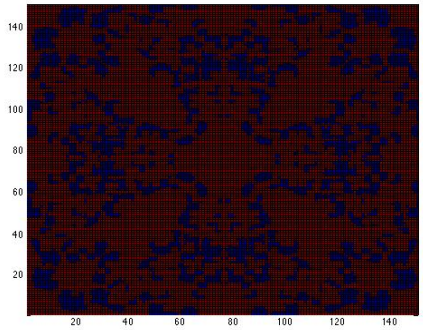
In this section we reproduce some of the qualitative features of the original results that were presented by Novak and May in [cite]. We consider a 151 by 151 grid. We require a grid dimension which is an odd number so that there is a central square into which we can introduce the single AD strategy at $t = 0$. This configuration best preserves the symmetry of the dynamics. A surprising result is that for certain values of b there is long term mutual coexistence of the strategies AC and AD. The range of values of b for which there is coexistence is relatively limited, with the approximate range of b being from 1.60 to 1.64 Below are simulation results for the case $b = 1.63$. At the beginning of the simulation there is a single AD individual at the centre of a grid otherwise populated by AC cells. The AD population expands outwards in a connected conglomeration. By the time they have reached the edge of the grid, the AD have formed the majority of the population. The spatial pattern is a dynamic and highly symmetrical one, likened by some to the design of Persian Carpets. Below we show some example plots to demonstrate the character of these patterns. The populations fluctuate about what appear to be well defined average values, being approximately 7,413 (32.5%) individuals for AC and 15,388 (67.5%) for AD. However, unlike our results, in this case the AD form a majority of the population.



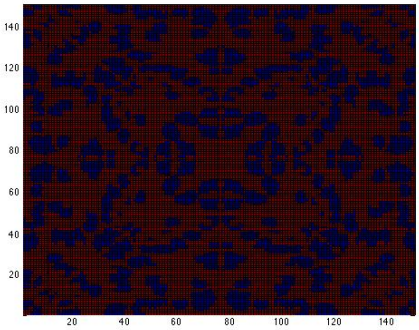
t = 20



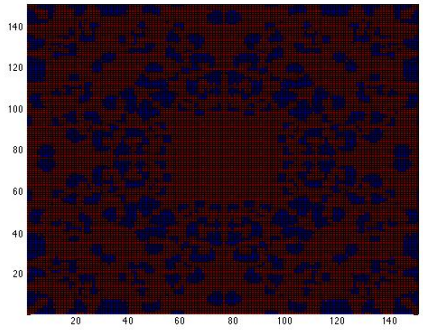
t = 50



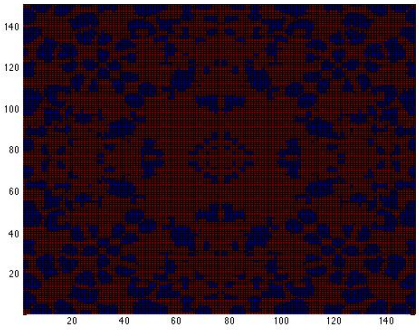
t = 300



t = 400



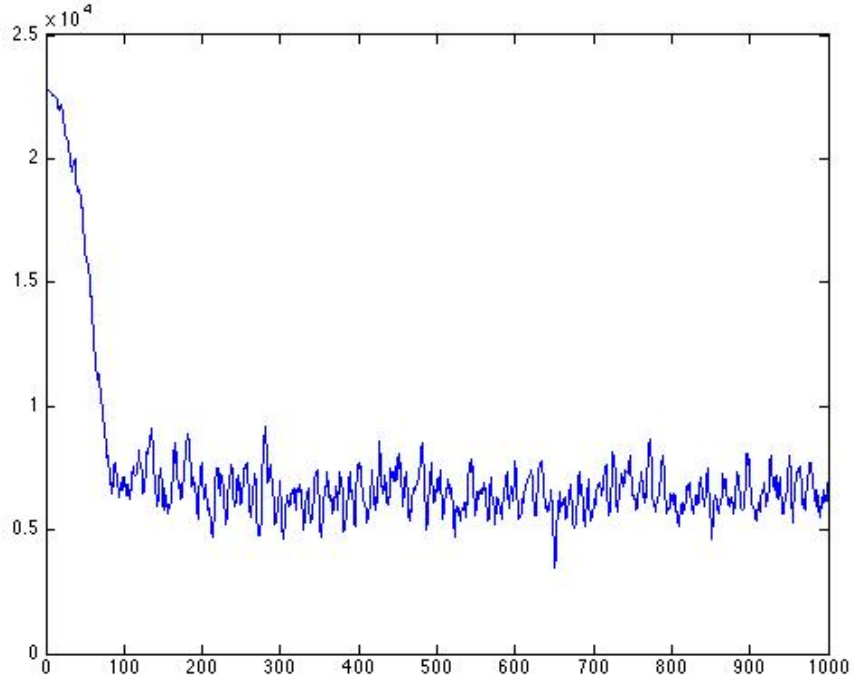
t = 500



t = 1,000

Table 3.1: Snapshots in time depicting spatial distribution of agents in a cellular automata realisation of the Prisoners' Dilemma with $b = 1.63$. The initial configuration at $t = 0$ is one AD at the centre of a grid surrounded AC. The dynamic symmetrical patterns that follow persist indefinitely.

Always Cooperate



Always Defect

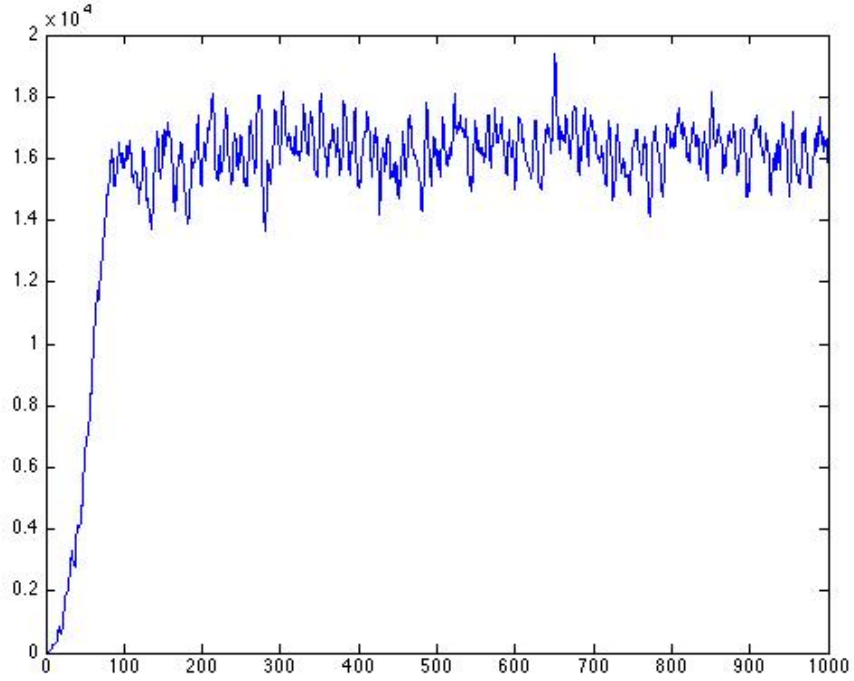


Table 3.2: Plots of population profile with time for cellular automata simulation of the Prisoners' Dilemma with $b = 1.63$. Mean AC population was 7,413 and mean AD population was 15,388. Standard deviations were 3,336 and 3,336. respectively.

The population profiles look similar in overall character to those we shall encounter for the individual based model of the Prisoners' Dilemma later in this thesis. The range of b for which these dynamic patterns persist is limited to $\frac{8}{5} < b < \frac{5}{3}$. For b above this range, the single AD colonizes the entire grid. For $1 < b < \frac{8}{5}$ there are small static of blinking colonies of AD that remain at the centre of the grid, and for $b \leq 1$ the AD rapidly become extinct. Within the range $\frac{8}{5} < b < \frac{5}{3}$ the dynamics are the same for each value of b, producing exactly the same patterns in exactly the same order. Thus a plot of any one value for b in this range serves to illustrate exactly the behaviour for all other values in this range.

It is interesting to note that the standard deviation in the size of the two populations is the same, at 3,336.

This example exhibits deterministically generated spatial structure. It demonstrates that spatial considerations may be important for understanding how different strategies might coexist even though some of those persistent strategies may not be Nash equilibria, or ESS's or stable under the assumption of a well mixed population.

This analysis may be applied to other two-player games such as the Hawk-Dove Game. Again in this case the proportions strategies present differ from that predicted by the analysis in Chapter 2, again demonstrating the importance of establishing the spatial structure of a population before being able to determine what strategy combinations may persist in any given population. We could also explore the effect of different initial starting conditions on the dynamics. It is also possible to introduce stochastic elements into the simulation, such as mixed strategies.

The Prisoners' Dilemma has been regarded as a metaphor for the problem of the evolution of cooperation. The goal of such analysis is to demonstrate under what conditions it is rational to choose to cooperate in this game. This has frequently led commentators to consider complicated conditional strategies, often with repeated encounters

with recognisable individuals. In this example we have considered no such sophisticated machinery. We have used only the two simplest basic strategies. Rational choices were not simulated. Yet these two strategies were able to coexist in a spatial domain. The fact that cooperators do well in the presence of other cooperators seems to be enough, under certain conditions, to allow cooperating sub populations to persist. This will also be one of the results of the individual based model to be described next.

Chapter 4

Outline of The Individual Based Model

Here we present in some detail the individual based model and highlight the assumptions involved. We start with an underlying continuum model that describes with partial differential equations the production and diffusion of a kairomone signalling chemical, and the diffusion movement and chemotactic response of the players, which we here interchangeably also refer to as agents. We consider the spatial domain as a grid, the points of which contain a discrete number of individuals. The underlying continuum partial differential equations are discretized using the standard five-point finite difference stencil. It is worth considering at this stage that the diffusion equation itself can be considered as a continuum approximation to a discrete random walk [153]. What we are doing here is going the other way, and deriving from a continuous model of a diffusion equation with chemotaxis a corresponding discrete random walk approximation.

4.1 Underlying Partial Differential Equations

The model used to govern agent movement is based on a system of partial differential equations. These are written in terms of the number of agents H_a of which there may be several types, indexed by a subscript a. There is a chemical kairomone field denoted by K and which naturally decays at a linear rate γ. The agents H_a each produce this chemical signal at a rate locally proportional to their concentration, with constant of proportionality ν_a. We are here allowing the rate of kairomone production to be different for different agent types. The movement of each agent is a diffusion (random walk) that is guided by the local kairomone concentration (chemotaxis). The sensitivity to the kairomone is denoted by χ_a which is permitted to be a different constant value for different agent types.

The governing equations and the non dimensionalization used are based on that in [25].

The Kairomone production, diffusion and decay is governed by:

$$\frac{\partial K}{\partial t} = \delta \nabla^2 K + \sum_a \nu_a H_a - \gamma K \tag{4.1}$$

And agent movement in the continuum limit is described by:

$$\frac{\partial H_a}{\partial t} = D \nabla^2 H_a + \chi_a \nabla . (H_a \nabla K) \tag{4.2}$$

Where δ is the kairomone diffusion constant and D is a random motility coefficient or diffusion coefficient, assumed the same for each agent type. Note in the case in which there is no kairomone field, then the movement of all agents will appear as a pure diffusion. Likewise, should any agent type H_a be insensitive to kairomone, then $\chi_a = 0$ and its spatial movement will be characterised as a pure diffusion, which in the

discrete approximation will correspond to an unbiased random walk.

All Agent types H_a sense local kairomone concentrations with a (possible zero) sensitivity χ_a and ascend kairomone gradients accordingly. The above equations are assumed to hold on a one hundred unit square and are already non-dimensionalized. Zero flux boundary conditions are applied. Numerical solutions utilised a standard explicit five-point central difference (finite difference) scheme. The one hundred unit square was divided into a one hundred by one hundred grid, yielding a grid spacing of $\Delta X = 1$. A time step of $\Delta t = 0.05$ was implemented, as compatible with the standard stability criterion for diffusive systems [153].

4.2 Individual Movement Rules

Each grid-point represents the location of a cell, inside which multiple agents may be located. At any given time the kairomone concentration at each cell is calculated from the above equation and is therefore known. In the following time step, agents may relocate to one of the four orthogonal nearest neighbour cells with a probability calculated from the explicit discretization of the equations above:

$$H_a(t+1)_{i,j} = P_0 H_a(t)_{i,j} + P_1 H_a(t)_{i+1,j} + P_2 H_a(t)_{i-1,j} + P_3 H_a(t)_{i,j+1} P_4 H_a(t)_{i,j-1} \tag{4.3}$$

Where the natural numbers i and j specify the coordinates of a given grid point. The probability coefficients P_0 to P_4 are given below:

$$P_0 = 1 - \frac{\Delta t}{(\Delta x)^2}\left[4\delta - \chi_a(K^{\tau}_{x+1,y} + K^{\tau}_{x-1,y} + K^{\tau}_{x,y+1} + K^{\tau}_{x,y-1} - 4K^{\tau}_{x,y}\right] \tag{4.4}$$

$$P_1 = \frac{\Delta t}{4(\Delta x)^2}\left[\delta - \chi_a(K^{\tau}_{x+1,y} - K^{\tau}_{x-1,y})\right] \tag{4.5}$$

$$P_2 = \frac{\Delta t}{4(\Delta x)^2}\left[\delta + \chi_a(K^{\tau}_{x+1,y} - K^{\tau}_{x-1,y})\right] \tag{4.6}$$

$$P_3 = \frac{\Delta t}{4(\Delta x)^2}\left[\delta - \chi_a(K^{\tau}_{x,y+1} - K^{\tau}_{x,y-1})\right] \tag{4.7}$$

$$P_4 = \frac{\Delta t}{4(\Delta x)^2}\left[\delta + \chi_a(K^{\tau}_{x,y+1} - K^{\tau}_{x,y-1})\right] \tag{4.8}$$

At each timestep, the equations are solved numerically to obtain the new kairomone concentration and probability coefficients. Probability ranges are computed by summing the probability coefficients to produce five ranges, R_0 to R_4 , where $R_0 = 0 - P_0$ and $R_j = \sum_{i=0}^{j-1} P_i - \sum_{i=0}^{j} P_i$.

A random number on the interval [0,1] is generated, and comparison with the above ranges will yield the agent motion for the next time step. (The possibilities being that the agent is stationary if said random number lies in the range R_0, will move left if in the range R_1, right if in R_2, up if in R_3 and down if in R_4). For all these simulations the following default parameters, [25], are applied unless otherwise stated:

Grid spacing $\Delta X = 1$

Maximum number of interactions per time step = 4.

Kairomone diffusion constant $\delta = 0.0005$

Kairomone decay constant $\gamma = 1$

Kairomone sensitivity $\chi = 0.0002$

Agent diffusion constant $D = 0.005$

Agent lifetime = 100

4.3 Individual Interaction Rules

We consider a population of agents, each of which is (genetically) programmed to use some particular strategy, i.e. its strategy is inherited.

Agents may only encounter one another when they are both on the same grid site. When agents encounter one another they engage in a single round of a game and are awarded payoffs according to the outcome. There is no limit to the number of agents that may occupy any given cell. An agent may engage in more than one round of the game in any given time step, against distinct opponents, up to a maximum user entered value (in this paper 4). This is the only limit placed on potential population size. The possibility of multiple interactions per individual per time step accentuates the effect of spatial inhomogeneities in the population distribution and was thus felt to be integral to the spatial nature of the simulation. However, the limit placed on the maximum number of interactions per time step represents an implicit limit on population size (or equivalently on the carrying capacity). Without such a limit populations may rapidly grow to uncomputational levels.

Throughout its life an agent accumulates payoffs. Each agent keeps a score of its accumulated payoff score. The payoff accumulated by an agent is to be identified with the fitness (number of offspring) of that agent. Agents with a large accumulated payoff will leave more offspring, so changing the composition of the population in the next generation.

For synchronous generation simulations, reproduction occurs at the end of an agents life. For non-synchronous generation dynamics, reproduction occurs whenever an agent has accumulated sufficient payoff to produce offspring.

The number of offspring produced is equal to the integer part of the said accumulated payoff. Offspring are deposited at the site occupied by the parent agent at the time of reproduction. Evolution of the system is observed in the sense of changing population strategy profiles. Agents have no memory of previous encounters. Therefore there can be no strategies that condition their actions on previous rounds of the game. Neither can there anything similar to a reputation. All interactions are therefore effectively anonymous.

The simulations may be run without kairomone secretion, in which case the movement of agents is a random walk based on a diffusion. However, it was considered interesting to allow some form of directed movement that might increase the searching efficiency of agents looking to interact with other agents. Unfortunately it was not possible to endow our agents with eyes, so some other method of directed movement was required.

As a mechanism known to operate in nature in host parasitiod systems, kairomone secretion seemed a natural and reasonable avenue to explore.

Although kairomone may diffuse to be detected at some distance from the source, it does not serve to discriminate between agents at the intra-cell level, which is to say that agents cannot distinguish the strategy to be used by their counterpart before the time of interaction. Agents cannot recognise the strategy of other players in advance of interaction. A high kairomone signal may be a sign that there are many of a particular type of agent near by, but within each cell all agents are anonymous and strategies cannot be distinguished in advance of interaction.

4.4 Mutations

The simulation code allowed for the possibility of mutations in various parameters. Mutation occurs at reproduction and happens when an agents offspring differ in some way from their parent. However, once created, an agent cannot itself experience mutation, we do not consider Lamarkian mechanisms. Kairomone production was allowed to mutate, allowing investigation of selection for increased or decreased kairomone production. A priori one might expect increased levels of kairomone production to be selected for when it is advantageous for agents to locate one another. In a situation where there is more than one agent type, more than one game strategy, there is likely to be a trade off between increased visibility to those with whom an interaction is beneficial and increased visibility to those whom might be more exploitative. For example, in a Prisoners' Dilemma simulation, it might be advantageous for Always Cooperate players to exude kairomone in order to more efficiently locate other Always Cooperate players with whom beneficial interactions will ensue, but this will also make these agents more visible to passing Always Defect agents with whom interaction would be harmful to their payoff scores and therefore to their fitness and number of offspring. In this case we are allowing each individual to have a different value for rate of kairomone production ν_a, so strictly each such parameter should also be indexed with a value unique to each agent.

The code also allowed for mutations in kairomone sensitivity χ_a. We could therefore run simulations in which agents of one type were producing and sensitive to kairomone, and examine whether there would be selection for a second strategy to evolve increased kairomone sensitivity in response. In this case we are allowing each individual to have a different value for rate of kairomone sensitivity χ_a, so strictly each such parameter should also be indexed with a value unique to each agent.

Also allowed were mutations in the strategies themselves. This was done by allowing

the agents to adopt mixed strategies, in which there is a probability that it will adopt a given pure strategy. By allowing these probabilities to mutate, one may be able to observe a population evolve.

Finally, the model provided for conditional strategies of memory one. Which is to say, simple strategies that choose from the pure strategies available depending on the previous move made against them, or depending on the previous move made by their opponent in its last round of play.

Chapter 5

Simulation Results for the Prisoners' Dilemma

The focus of much work on the Prisoners' Dilemma has consisted of attempts to explain the origin of cooperation from an environment of defectors. The basic rationale being that the default behaviour of an individual under selective pressures should be to defect, and from this starting point the goal has been to derive a viable cooperative strategy that can survive or even replace the native defecting contingent.

The issue of cooperation in nature is not restricted to social evolution. Cooperation is necessary at many levels in biology, from the aggregation of cells to form larger bodies, to the assemblage of organs to the behaviour of slime moulds and insect societies. Interesting examples of Prisoners' dilemma type situations in real biological systems include the external digestion of sucrose by yeast [82].

One mechanism for the evolution of cooperation between different species is what is called mutualism, in which a cooperative interaction results in benefits to both organisms. Mutualism is thought to underlie the evolution of approximately half of all

terrestrial plants, which rely on symbiotic relations with fungi to obtain nutrients, usually in their root systems [115], and is generally acknowledged to have played a major role in the development of biological diversity generally. Spatial effects in the evolution of mutualism, including the role of dispersal ranges, have been addressed via a lattice model in [114].

In this work we consider essentially parasitic interactions, in which one party profits at the expense of the other. Such may in some sense seem to be the polar opposite of mutualistic interaction in which both parties benefit. However, it seems likely that some extremely close, even symbiotic, relationships, such as that between a eukaryotic cell and its mitochondria, may have had their origin in an interaction that was initially parasitic in nature.

A real biological system that exhibits Prisoners' Dilemma type behaviour has been reported in [97]. Here the authors were able to identify a convincing measure of fitness in a system of E. coli bacteria with different strategies for nutrient conservation during hardship. The authors note that their example extends "the application of the prisoner's dilemma to prokaryotes, emphasizing the generality of this model in describing biological interactions in diverse organisms." From the host-parasite point of view, the effect of spatial structure and the contrast with a well mixed population was investigated by [101] in which the host was the bacterium E. coli and the parasite a T4 phage. Their result was in general accord with spatial ecological models, in that the parasites in the well mixed population evolved to be more virulent than those in the more locally structured environment. In an experimental study, [103] have adjusted the viscosity of the food medium for larvae of the Indian Meal Moth. This has the effect of adjusting the dispersal of the larvae, with a hard food medium leading to clustering and low dispersal, and a more fluid medium promoting increased dispersal. These organisms were exposed to a viral infection and it was found that host infectivity decreased in the hard food medium and increased in the soft medium. This being in general agreement with

the theoretical expectation that virulence should decrease with decreased host dispersal. In a sense we can regard the pathogens in this experiment as cooperating in the less dispersed larvae population by collectively reducing individual virulence in order not to cause excessive damage to the supply of hosts. Further examples of Prisoners' Dilemma type interactions in nature in which conditional or reciprocal strategies may be at work, have been discussed in various references, see for example [155], [154] and in particular work on stickleback fish [157] and vampire bats [156] have indicated other Prisoners' Dilemma type strategies such as Tit For Tat. The founding reference in this field is the work of Trivers [11].

The importance of considering biological and ecological interactions in an explicitly spatial environment has long been recognised. In a well mixed game theory interaction of the Prisoners' Dilemma type, the introduction of even an infinitesimal contingent of defectors into a cooperating population would have an immediate and detrimental effect on the entire co-operating population. By embedding the agents as discrete entities in space, we would expect that it might sometimes be possible for cooperating strategies to tend to build clusters of similar individuals. These may be sustained by virtue of local interaction and reproduction. Such clustering could protect cooperative populations from the negative effects of defectors, while at the same time enhancing the cooperators payoff through their mutual interactions. Furthermore, this clustering effect need not be introduced by hand via any specific mechanism for that purpose, but instead may arise naturally as a mere consequence of embedding interactions in space. We shall find that the correlations that result simply due to spatial distribution can for some parameter ranges allow for coexistence of pure strategy types, simply because such correlations will determine who plays with whom, (see [57] for a more complete review). So in a spatial Prisoners' Dilemma for example we may expect to find parameter regions in which there is a coexistence of the strategies Always Cooperate and Always Defect.

In terms of graph theory, the well mixed case is analogous to the complete graph case, in which individuals occupy the vertices and the network of contacts is defined by the connecting edges. The square grid cellular automata models correspond to an arrangement of agents at the vertices of a regular graph of degree 4. The work of Novak and May [21], [22] can be viewed in these terms.

This thesis seeks to formulate game theory type interactions is a spatial domain. It was inspired by the work of Chaplain, Schofield and Hubbard on individual based models applied to host-parasitiod systems,[25], [26]

Following Nowak and May [21], [22], [23], we assigned very small values to S and P, such that they may be neglected as potential contributions to any accumulated payoff. This is to say that the payoff for mutual defection, and for a cooperator against a defector is to be unproductive in terms of its contribution to future agent progeny. Indeed, were we to set $P = S = 0$ then the essential characteristics of this prisoners dilemma would be unaffected in this situation, [24].

A payoff matrix was chosen such that the AC agents would be capable of a self-sustaining population. The AD, being extremely unlikely to gather sufficient payoffs from their encounters with other AD during their lifetime would not be capable of sustaining a population among themselves, but could gain sufficient score to reproduce from interactions with AC players. In this way one can regard AD as parasitic upon the AC population.

As is standard with models of this type, the parameter space is vast, so nothing like a complete catalogue can be given here. Rather we have sampled such values as seem to exhibit interesting results and that hint at the variety of behaviours that may be obtained.

The initial configuration considered will usually consist of 50,000 individuals, a single

Always Defect at the centre of a randomly scattered population of 49,999 Always Co-operate. This might be interpreted as the centre of an outbreak of disease or parasitism.

Initially we shall consider a case with one set of payoff matrix parameters and examine the effects of kairomone secretion and synchronous and non synchronous generations. We will then examine how the dynamics changes in response to alterations in the pay-off structure.

We examine in detail the dynamics arising from the payoff matrix values set as follows: $T = 0.07$, $R = 0.02$, $P = 0.001$, $S = 0$, so the payoff matrix is written as:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 0.02 & 0 \\ 0.07 & 0.001 \end{pmatrix} \end{array} \tag{5.1}$$

The dynamics ensuing from this particular payoff matrix leads to stable coexisting populations under a wide range of conditions.

We then comment on the effect on the dynamics of varying T, which can be viewed as parameterizing the advantage of cooperation over defection as a strategy against a cooperative player. In this case the minimum value T may assume is 0.02, which is the case $T = R$. Increasing T amounts to increasing the productivity to AD of an encounter with AC. Thus we would expect that this should contribute to increasing the number of AD progeny in the next generation. Increasing T is akin to allowing the outbreak of parasitic AD to become more virulent. We would expect that for high values of T and therefore very virulent AD the AC host population will be severely depleted, and that this will in turn have the effect of curtailing the AD population. For extremely high T the AD population will become extinct as the AC population becomes unable to sustain the parasite burden.

Simulations were run for 500,000 time steps, which is equivalent to 5,000 generations.

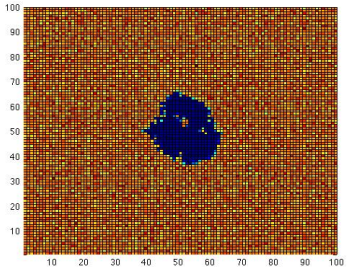
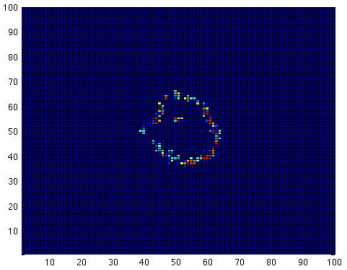
5.1 Synchronous Generations

Without Kairomone Secretion $(\nu = 0)$

The single central AD gives rise to an almost circular expanding wavefront of AD agents. This wavefront is relatively thin and therefore leaves a few surviving AC in it wake. A small population of AD also persist behind the wavefront. This co-existing population behind the initial wavefront itself expands outwards to fill the devastation in AC caused by the initial advancing AD. This residual population thereby manages to re seed the grid, yielding a dynamic and fluctuating spatial pattern of AC closely followed by flocks of parasitic AD. The grid remains sparsely populated. The AC are distributed in fluctuating clumps which expand and move across the grid, growing until they encounter a local population of AD, after which there is severe and rapid decline in local AC numbers. The AD population appears to be distributed as small fragmented filamentary wavefronts. The scattered patchwork of population centres appear to move and then disappear as others grow elsewhere to take their place.

Both population levels appear to fluctuate about stable well defined average values. Time average population values after 500,000 time steps (5,000 generations) were 82,141 for AC and 24,011 for AD, constituting 77% and 23% respectively. The stability of the populations was surprising. Population standard deviations were 37,331 and 3,339 which confirm that the fluctuations in population levels, not being of the same magnitude as the average population itself, did not threaten the long term viability of the coexistence. The fluctuations evident in the population plot and the standard deviation figures show that the populations were relatively stable about their average values.

The carrying capacity for AC in the absence of AD was 366,000. Thus the AD were very efficient at regulating the AC population to a stable but much reduced level of some 22% of the carrying capacity in the absence of AD.

Always Cooperate	Always Defect
	
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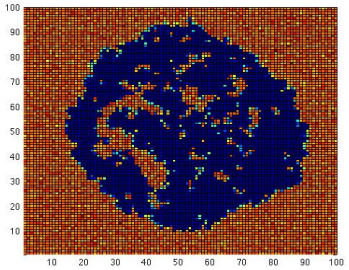	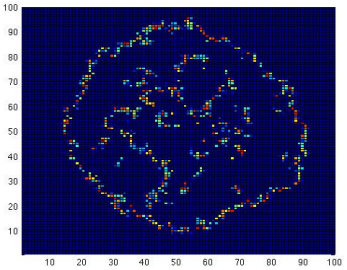
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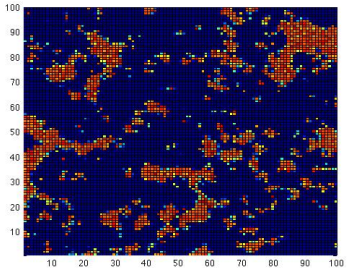	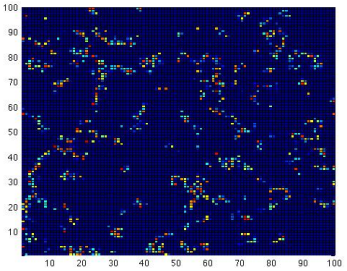
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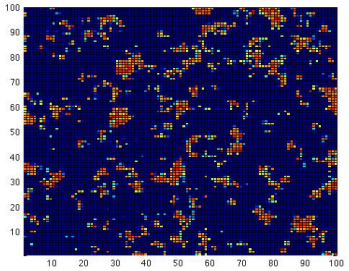
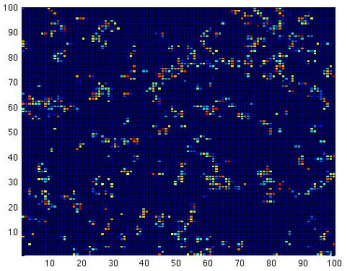
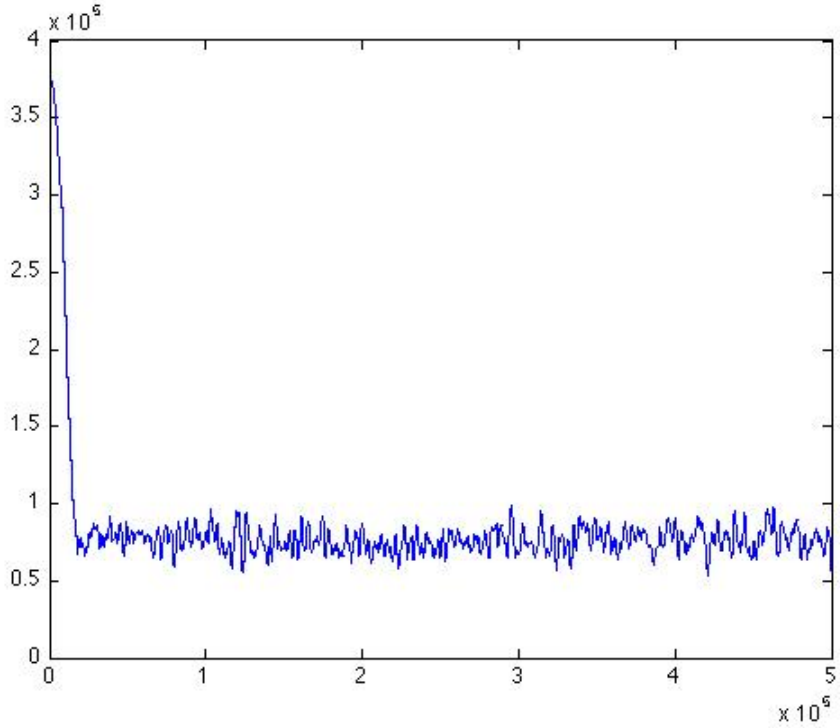
	
t = 500,000	t = 500,000

Table 5.1: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC.

Always Cooperate



Always Defect

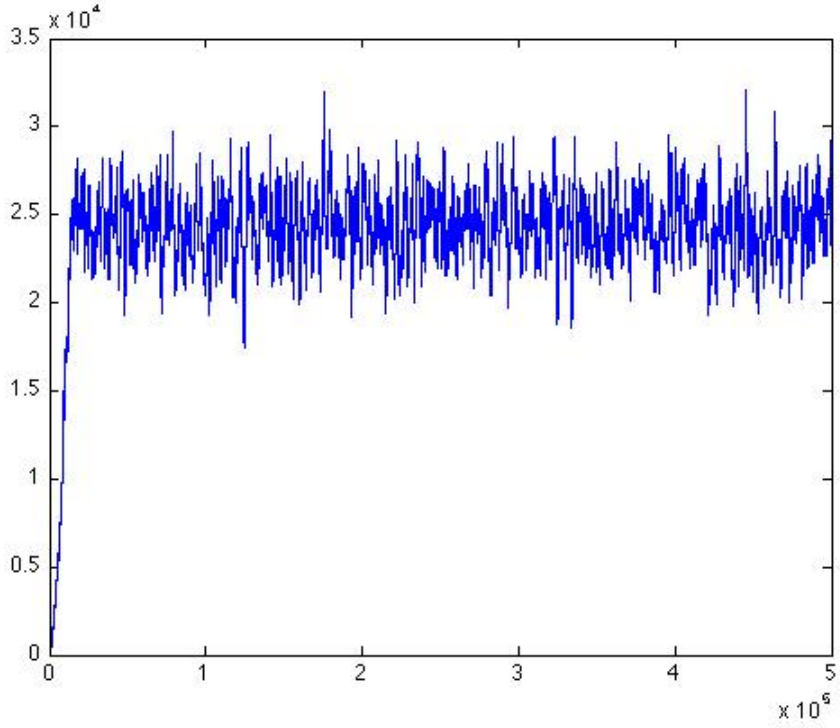


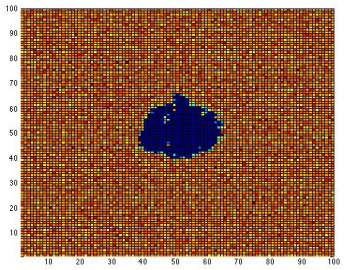
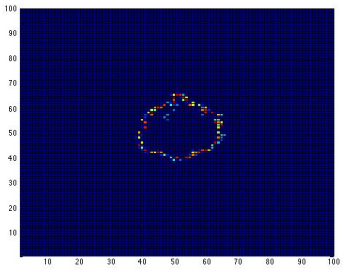
Table 5.2: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of AD = 24,011, mean number of AC = 82,141. Standard deviations in the AD and AC populations are 3,339 and 37,331 respectively.

With Kairomone Secretion, $(\nu = 1)$

The simulation starts as before, with a wavefront of AD advancing through the AC population leaving mostly unoccupied grid space in its wake. Again, several small local populations of both strategies survive behind the initial wavefront. The residual population is sparser and the AD more clumpy than in the above without kairomone case, with more unoccupied space. The AD form longer filamentary structures, appearing as small spiral wavefronts that expand into the the AC populations, wiping them out.

Again both populations are inhomogeneously distributed in space and both exhibit oscillatory fluctuations about a stable long term average. The average AC population is higher than the previous case at 86,869 individuals, whereas the AD population is depressed to 13,538 individuals. This represents a population split of 86.5% to 13.5%.

In this simulation kairomone secretion seems to act the detriment of the AD population, whose size becomes roughly half that of the non-kairomone case.

Always Cooperate	Always Defect
	
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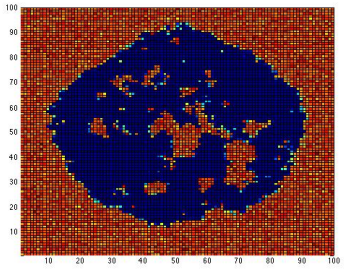	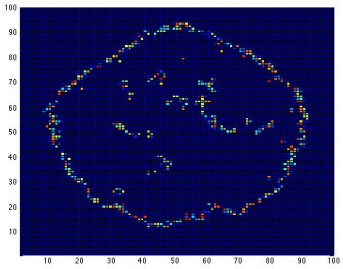
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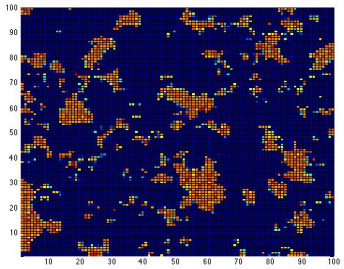	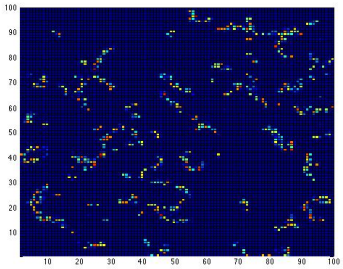
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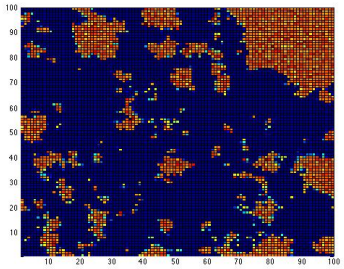	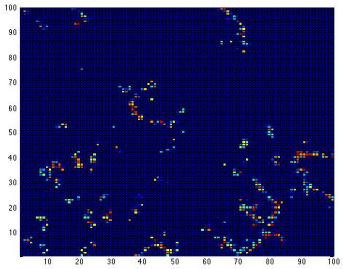
t = 500,000	t = 500,000

Table 5.3: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC. After the initial invading wave of AD reached the edges of the grid, both AC and AD populations persist, but at low levels, with the AC moving through the grid and the AD in pursuit.

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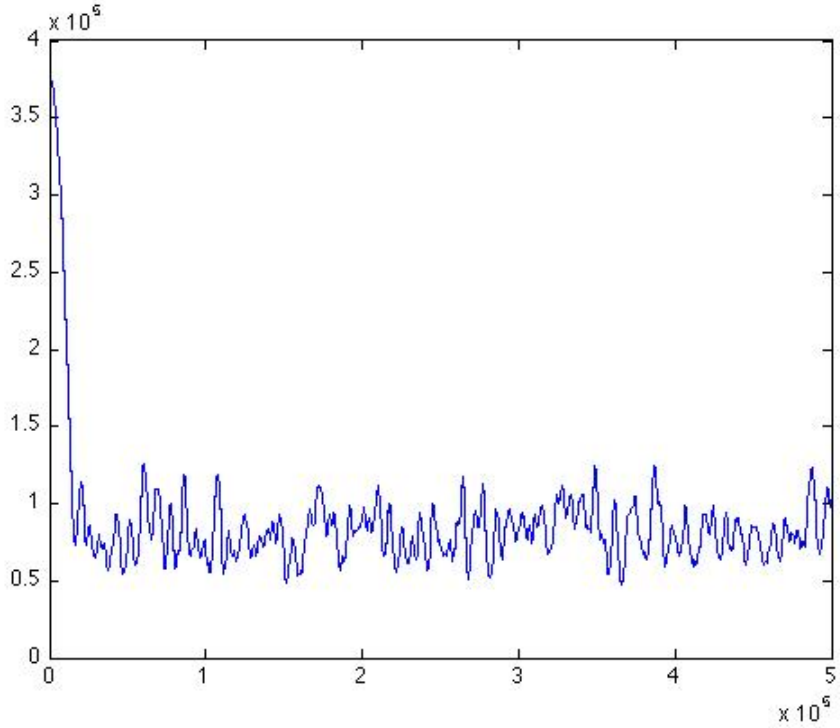

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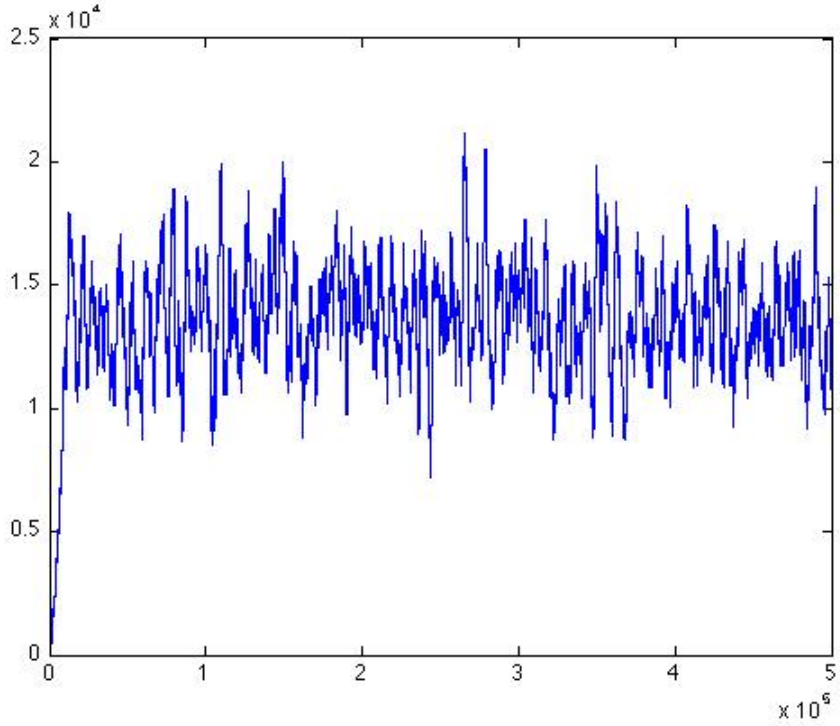

Table 5.4: Plots of the agent population in time. The populations exhibit long term co-existence, though oscillations in this case are substantial. Mean number of AC = 86,869, mean number of AD = 13,358. Standard deviations in the AC and AD populations are 38,688 and 2,403 respectively.

Kairomone production for AC only ($\nu_{AC} = 1$)

Here we investigate the effect of having the AC agents be the sole source of kairomone. This situation may perhaps more closely match the analogue in which we regard the AD as parasitic on the AC. The stable average for the AC population is 81,281 and for the AD population is 12,710. The average percentage population composition was therefore the same as the previous case, being 86.5% AC and the remaining 13.5% AD. The spatial character of the two simulations was also very similar, with relatively large conglomerations of AC being sparsely distributed amongst an even more sparsely distributed AD population. The AD agents formed very small traveling population centres that grew rapidly in number whenever a substantial AD population was chanced upon. It would thus seem from this example that the secretion of kairomone by the AD has very little effect in an environment in which the AC are kairomone secreters. Or to put it another way, if kairomone secretion is allowed then the major effect is on the interaction between AC players.

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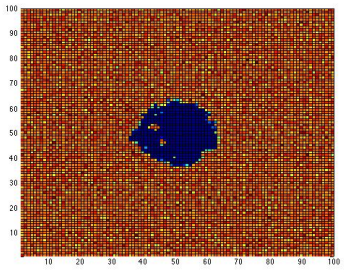	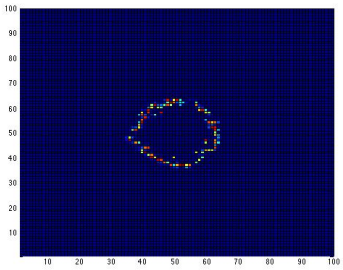
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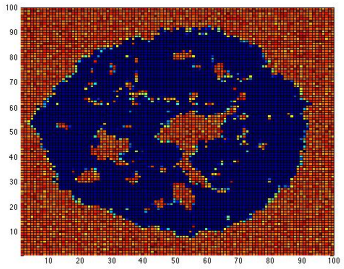	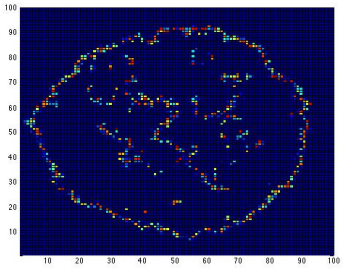
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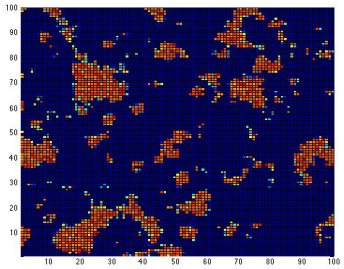	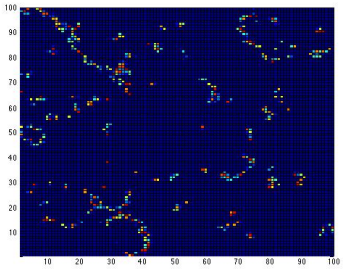
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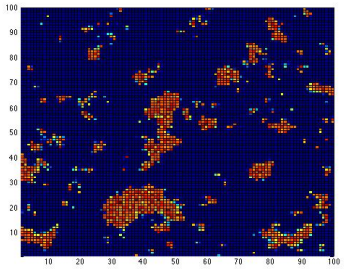	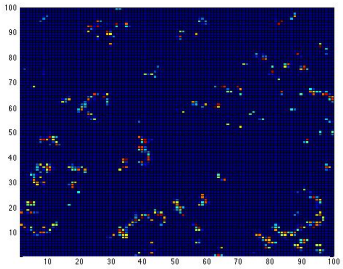
t = 500,000	t = 500,000

Table 5.5: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion for the AC agents only ($v_{AC} = 1$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC. After the initial invading wave of AD reached the edges of the grid, both AC and AD populations persist, but at low levels, with the AC moving through the grid and the AD in pursuit.

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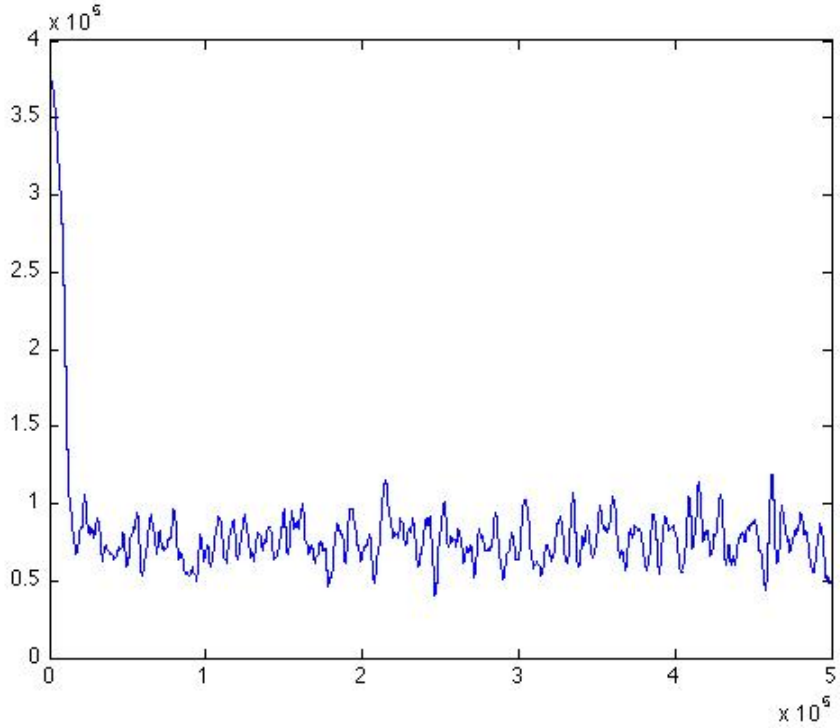

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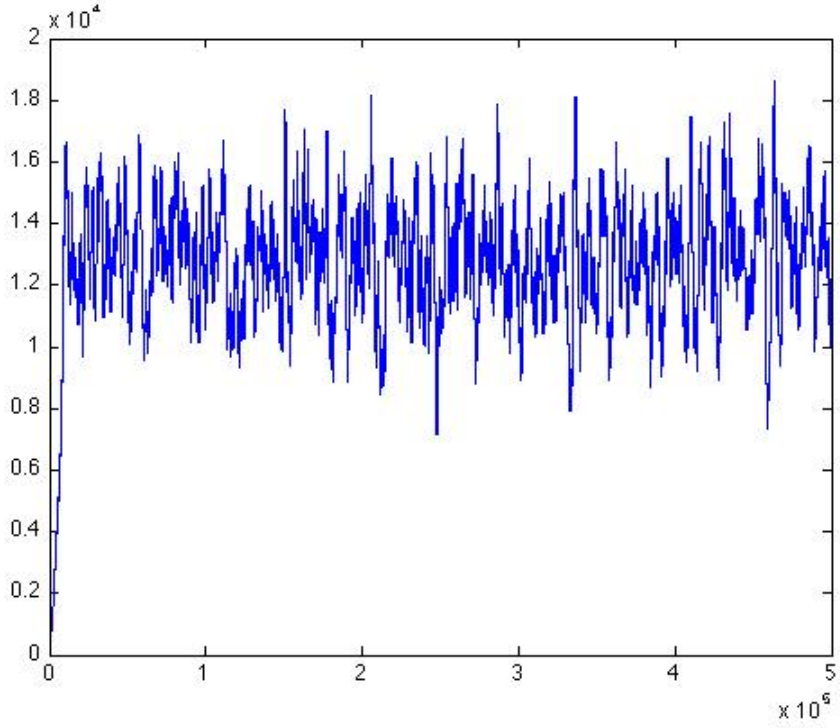


Table 5.6: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of AD = 12,710, mean number of AC = 81,281. Standard deviations in the AD and AC populations are 2,124 and 37,542 respectively.

Discussion

As is evident from the population plots and the standard deviation figures, neither agent type was in danger of extinction for the five thousand generation course of the simulations. Of course, it is always possible that had we run for a greater length of time then one or other population may have crashed. But it seems reasonable to remark that both populations were notably resilient. Furthermore, both agent types exhibited fluctuations about what appeared to be stable long term average population levels.

A population composed exclusively of AC agents stabilises at around the level of 366,000 individuals. We consider this to be the carrying capacity of the grid. The AD by contrast cannot form a stable monomorphic population. However, the AD can survive in the presence of, and also to the detriment of, an AC population. In this sense we can consider the AD to be parasitic on the AC agents. The presence of the AD therefore act to suppress the AC population.

The contrast between these simulation runs shows the effect of kairomone secretion. Kairomone production by the AC causes it to be slightly less fragmented, more clumpy. Kairomone productivity seems to increase the efficiency with which the AC can locate one another which would lead to an increase in mutually beneficial AC-AC interactions. This is reflected in a slightly increased average population, with levels being elevated by approximately 5% for the with kairomone population compared to that without kairomone. The AD do not fair so well in the kairomone secreting environment, with population levels declining by about 55%. In the presence of kairomone the AD population becomes considerably sparser, and forms more extended filamentary or spiral wavefronts. One reason for the decreased levels of AD may be that the increased clumpiness of the spatial distribution of the AC leaves more empty voids on the grid, making it more difficult for small surviving colonies of AD to travel to the next local maximum in the AD population. Another factor is that since the AD

are also kairomone producers, they will be locally more biased to move towards one another and thereby into an increased number of unproductive AD-AD interactions. The presence of the AD agents acts to suppress the AC population to some 22.4% of its carrying capacity level in the case on no kairomone secretion, and to 23.7% of its carrying capacity value when kairomone is indiscriminately secreted. On balance, indiscriminate kairomone secretion is beneficial to the AC and detrimental to the AD.

If we arrange that only the AC are kairomone secreters and the AD do not secrete kairomone but remain sensitive to it, then there results a spatial distribution of AC and AD agents that is broadly similar to the case of indiscriminate kairomone secretion. However populations of both agents were found to be lowest for this simulation, with AC averaging at 81,281 individuals and AD at 12,710, corresponding to a population split of 86.6% to 13.4%. In this case the AD are more effective at suppressing the AC population, albeit also at some cost to their own numbers as increased efficiency in finding AC also translates in to reduced AC numbers and hence a sustained decreased in the AD population, by 53% from the zero kairomone case. The AC population however remains at around 99% of its value in the zero kairomone situation. Interestingly, not allowing the AD to produce kairomone leads to a lower AD population than if we do allow AD kairomone secretion, with the population level in the former case being 93% of that in the latter. This is counter intuitive for one would expect AD kairomone secretion would increase the number of unproductive AD-AD encounters.This may be because AD kairomone secretion attracts AC players to regions of AD concentration.

Table 5.7: Comparison of Simulation Results for Case $T = 0.07$, $R = 0.02$

Case	Kairomone (v)	AC Mean	AD Mean	Comment
1	0	82,141 (77%)	24,011 (23%)	Coexistence
2	1	86,896 (86.5%)	13,358 (13.5%)	Coexistence
3	1 for AC only	81,281 (86.5%)	12,710 (13.5%)	Coexistence

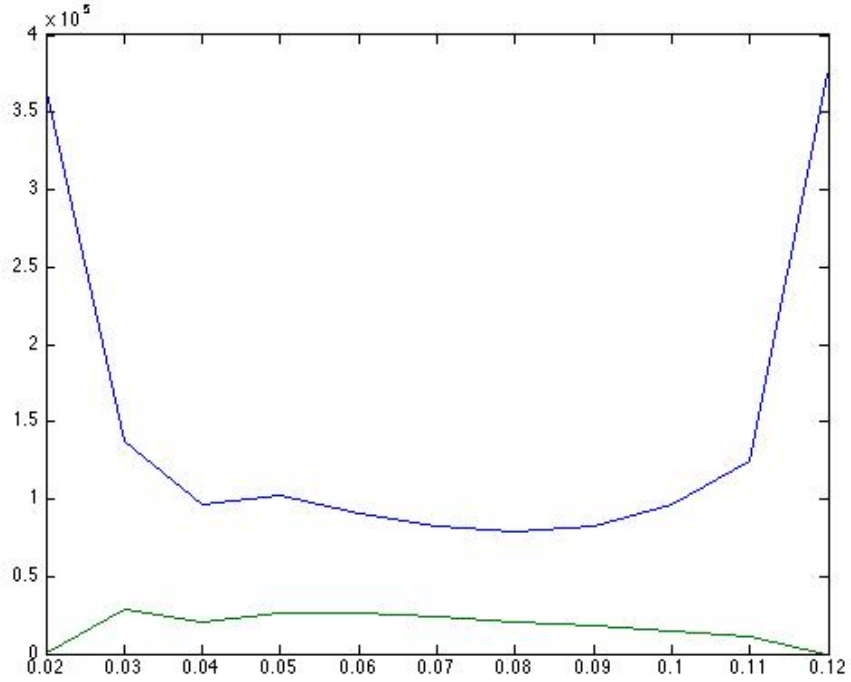
The Effect of Varying T

Simulations were run with different values of T, the lowest admissible value here being 0.02 and corresponds to an AD gaining the same payoff from AC and AC gain from interacting with each other. In this case we would expect that the AD would eventually become extinct, as they would be disadvantaged in their interactions with one another, in which they would gain a payoff close to zero. In such a population the AC should have a survival advantage. Increasing the value of T would be expected to open a window in which the AD can profit from a higher payoff against AC than in AC-AC interaction. However, increasing T by too much should lead the AD to assume some likeness to a virulent infection that, in profiting too greatly at the expense of the AC, will so depress the numbers of cooperators that the AD will themselves suffer as their prey/host numbers become unable to sustain the AD burden. In the below plot, table 5.8, we show how the average population values for both agent types varies with the payoff parameter T. At the extreme low end, where $T = R$, the AD eventually become extinct, being out competed by the AC who will have a competitive advantage by virtue of their mutually beneficial interactions. Here the AC long term average will therefore be the carrying capacity of the grid, which was around 366,000. As we begin to increase T, the AD find a niche in which they may exist as exploiters of the AC, and this causes a substantial decrease in AC numbers. There is a stable invasion of an AD minority. As T increases further, the AD become more virulent and at around $T = 0.12$ the AD cause such harm to the local AD population that there is not enough left to sustain possible future generations of AD and they therefore become extinct.

As we increase T, the fluctuations in both populations increase, for the virulence of the AD will locally have a severe impact on AC numbers, while local populations of AD will boom on encountering clusters of AC, but this will then leave their progeny with relatively few hosts with which to sustain future generations. Below is a population

plot for both agent types for the case $T = 0.11$. This is right on the edge of the range of T for which stable long term coexistence was found possible. Note the size of the fluctuations about the mean indicate that the populations are sometimes approaching close to extinction.

Population as a Function of T



Percentage Population Composition as a Function of T

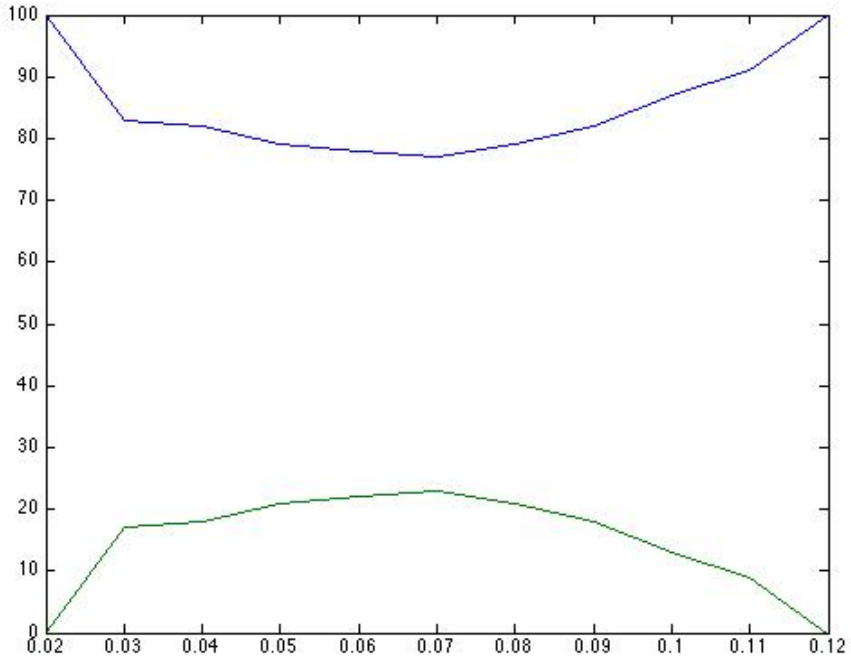
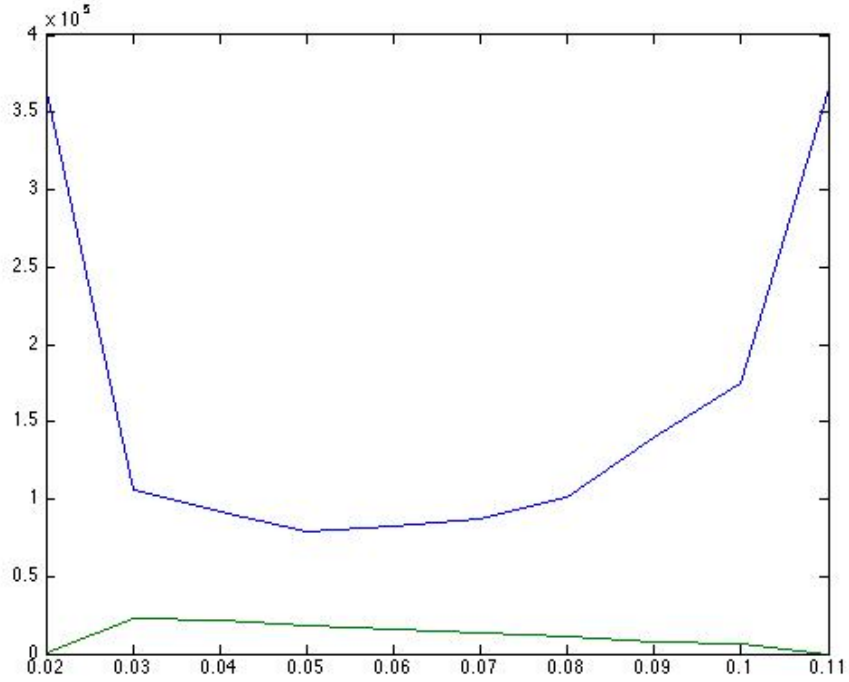


Table 5.8: The case of no kairomone secretion. As T increases from its minimum possible value of 0.02, the AC population falls in response to a stable invasion by a minority of AD. As T increases further the AD become too virulent for long term viability.

Population as a Function of T



Percentage Population Composition as a Function of T

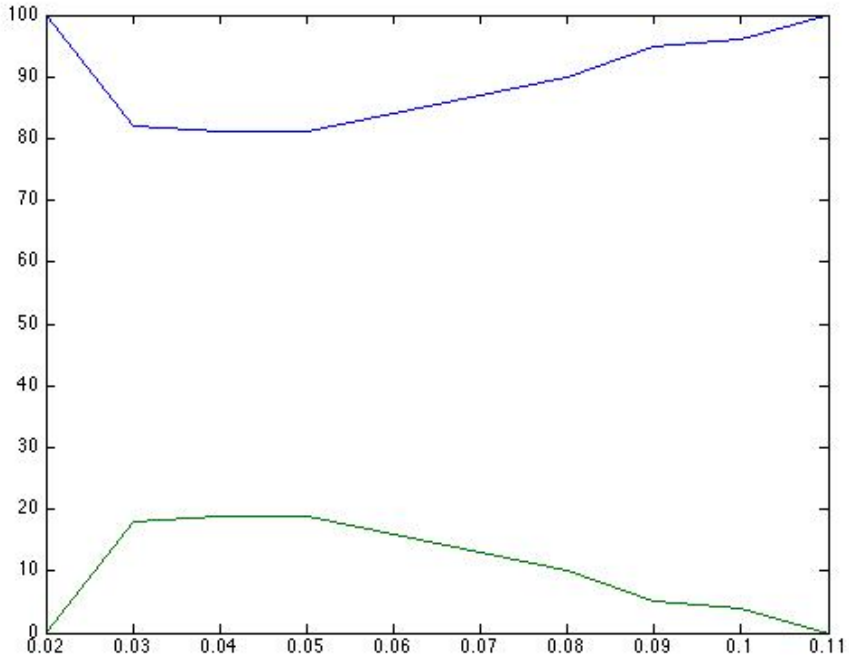


Table 5.9: The case with kairomone secretion. As T increases from its minimum possible value of 0.02, the AC population falls in response to a stable invasion by a minority of AD. As T increases further the AD become too virulent for long term viability.

Comparing the plots for the two cases of with and without kairomone, it is clear that the presence of kairomone is somewhat destabilising for the mutual coexistence of the two strategies. Keeping all else equal, switching on kairomone secretion reduces the range of values of T for which coexistence is possible. Without kairomone we have coexistence up to $T = 0.11$ whereas in an environment of indiscriminate kairomone secretion mutual coexistence is observed only up to $T = 0.9$. In both cases the AD remain effective at restricting the AC population to significantly below the grids carrying capacity.

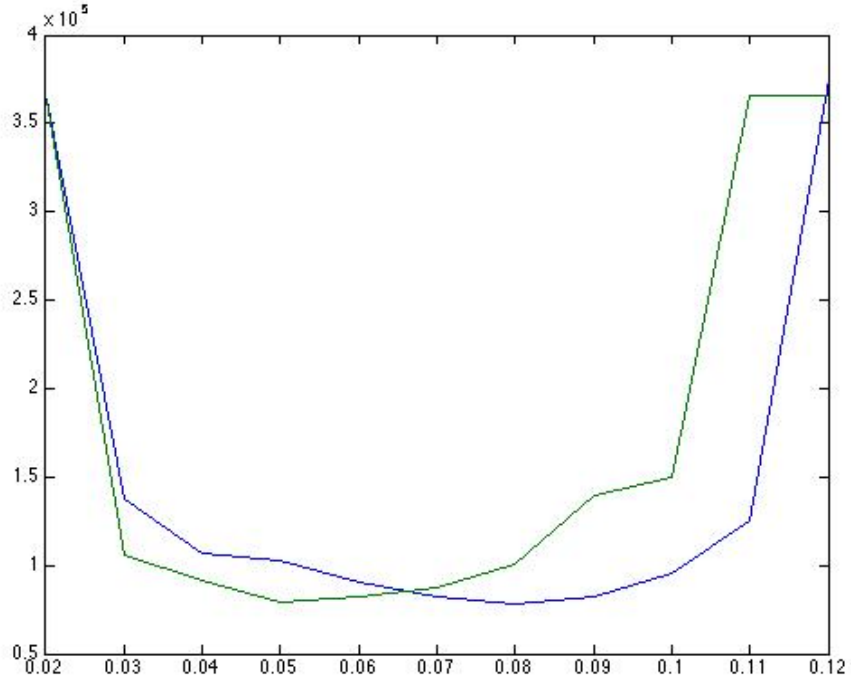
The below plots, table 5.10, compares directly the numbers of AD and AC agents in each population for the two kairomone scenarios. The top graph in table 5.10 shows that qualitatively the AC population plots are similar, except for the fact of the reduced range of coexistence for the kairomone case means that the AC resume their carrying capacity for lower values of T. The bottom graph in table 5.10 shows the reduced range for which the AD population is viable in the case of a kairomone environment. It is also apparent that in absolute terms the AD numbers are higher in the zero kairomone environment. This confirms the above analysis that mentioned that overall, kairomone secretion is detrimental to AD numbers. Which is to say, it is detrimental to the parasitic strategy. This is surprising as it was expected that the kairomone should allow directed movement of the AD towards centres of AC and therefore kairomone was initially expected to act to the benefit of the AD. One reason for this outcome is that kairomone secretion allows for more densely clumped AC. This then increases the amount of grid space that is unoccupied by the AC. This in turn can make it more difficult for the AD to locate AC agents as they will have on average further to travel to the next AC population concentration.

To better simulate the situation obtaining in real host parasitoid interactions, it might be instructive to re run these simulations with AC kairomone secretion but with AC kairomone sensitivity set to zero. In this case the AC will be producing kairomone

that the AD will be able to sense. But the AC themselves will not be able to sense kairomone and therefore should not form such an inhomogeneous spatial distribution on the grid. This may give more of an advantage to the AD.

The final set of graphs in this subsection, table 5.11, is a population profile in time for the largest value of T for which long term coexistence is observed. This occurs for the non kairomone case with $T = 0.11$. The coexistence is becoming increasingly unstable at this point, with wild population fluctuations for both agent types. On at least one occasion the AD numbers become perilously close to zero. In the course of this simulation the AD numbers recovered but it is not hard to imagine that in other runs the AD may actually have become extinct.

AC Population as a Function of T for both kairomone and no kairomone



AD Population as a Function of T for both kairomone and no kairomone

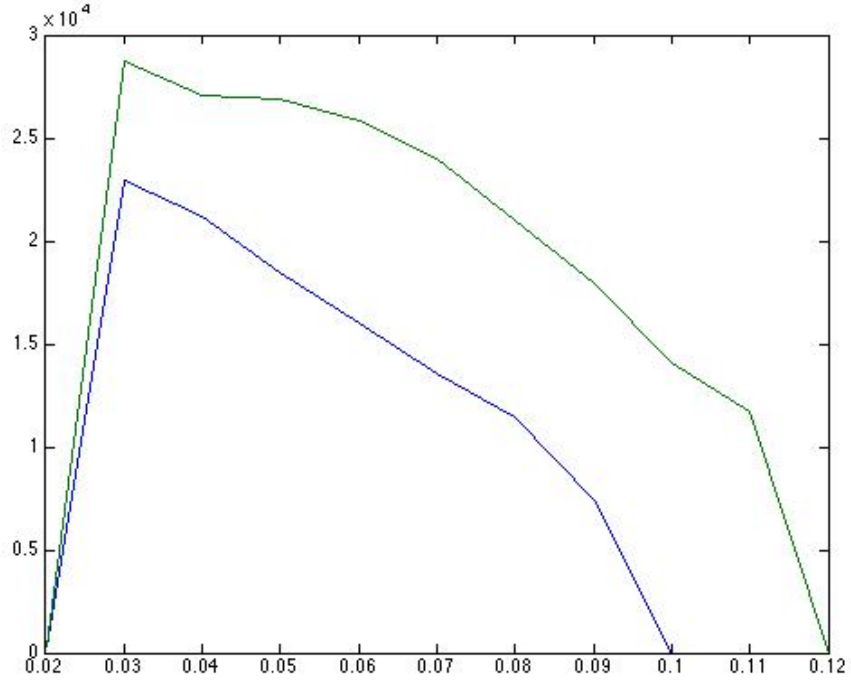


Table 5.10: The case with kairomone secretion. As T increases from its minimum possible value of 0.02, the AC population falls in response to a stable invasion by a minority of AD. As T increases further the AD become too virulent for long term viability.

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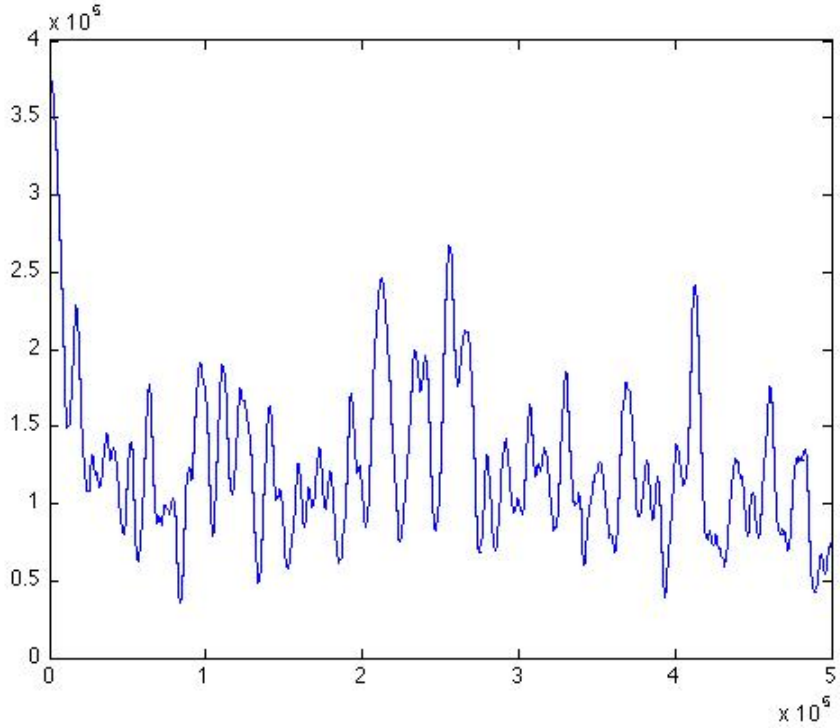

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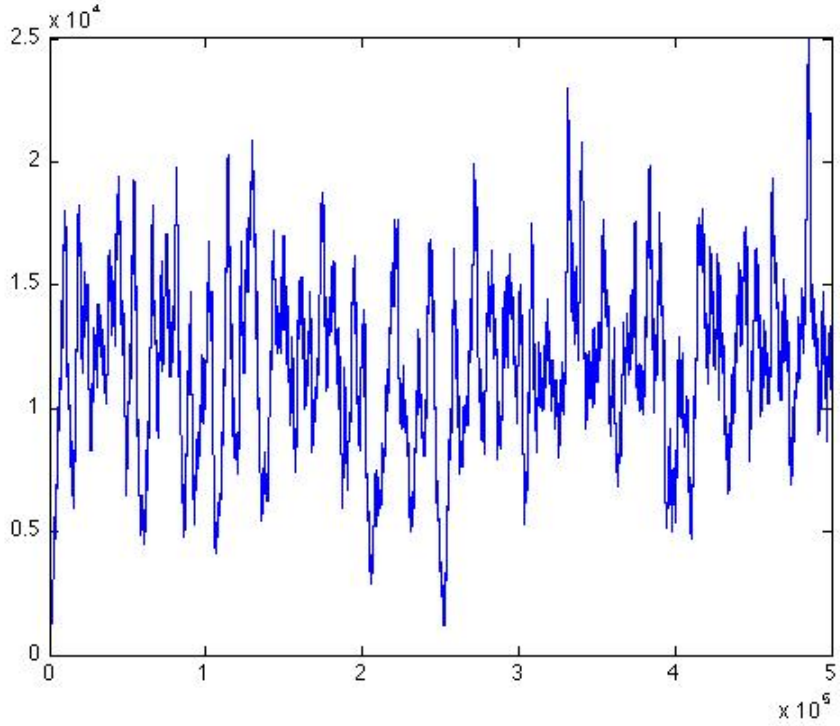

Table 5.11: Plots of the agent population in time for the case $T = 0.11$. The populations exhibit long term stable co-existence, each oscillating about a stable long term average. Mean number of AC was 124,810 (91.4%), the mean number of AD was 11,690 (8.6%). Standard deviations in the AC and AD populations are 50,863 and 3,523 respectively.

5.2 Non-Synchronous Generations

Without Kairomone Secretion, $(\nu = 0)$

In this case the AD wavefront expands faster into the AC population than compared with the corresponding synchronous case. In its wake there are again left residual populations of both agent types, which move and interact to yield a dynamic pattern. The AC form expanding clumps whose growth is curtailed by small advancing fragmented filamentary spiral wavefronts of AD. Compared to the synchronous case, the AC population is increased by 27% from 82,141 to 104,170 individuals. The AD population is more clumpy than in the synchronous case. AD numbers on the other hand fall by 37% from 24,011 to 15,131. By comparison, the AD population is more sparsely distributed for non synchronous generations.

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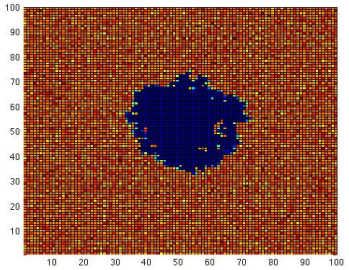	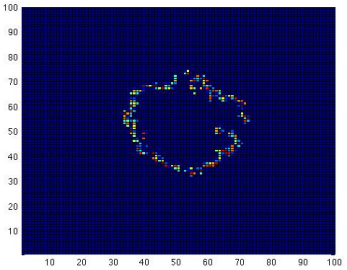
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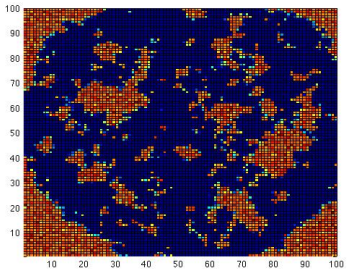	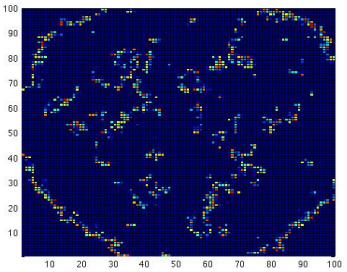
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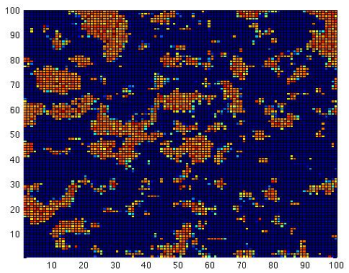
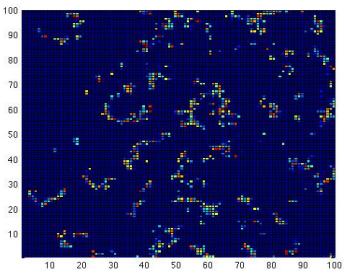
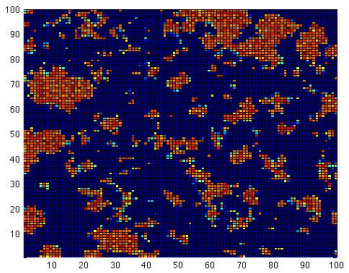
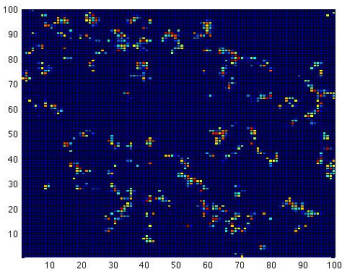
	
t = 100,000	t = 10,0000
	
t = 500,000	t = 500,000

Table 5.12: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC. The grid is sparsely populated by both agent types, with AC being present at far below the grid carrying capacity.

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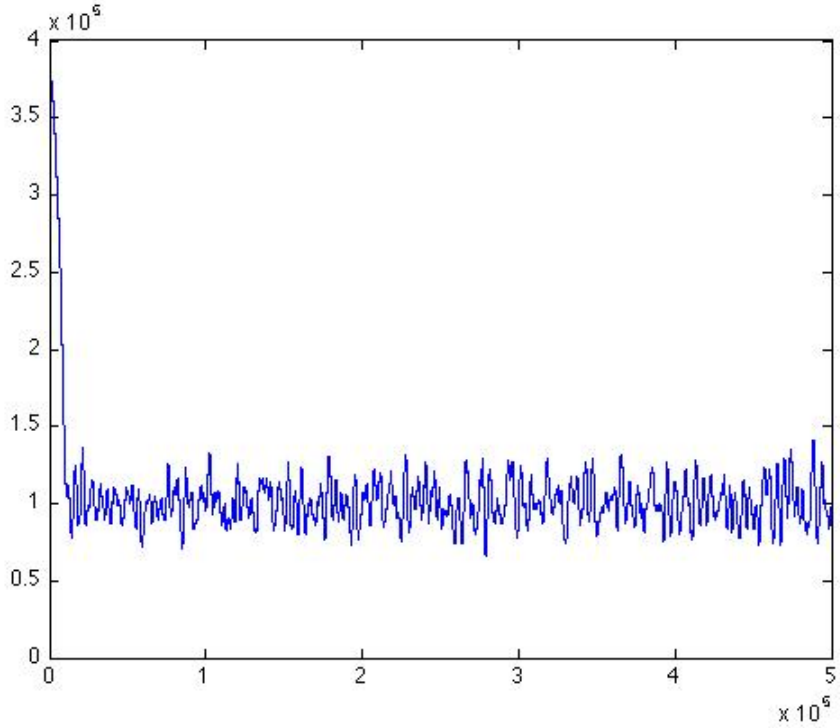

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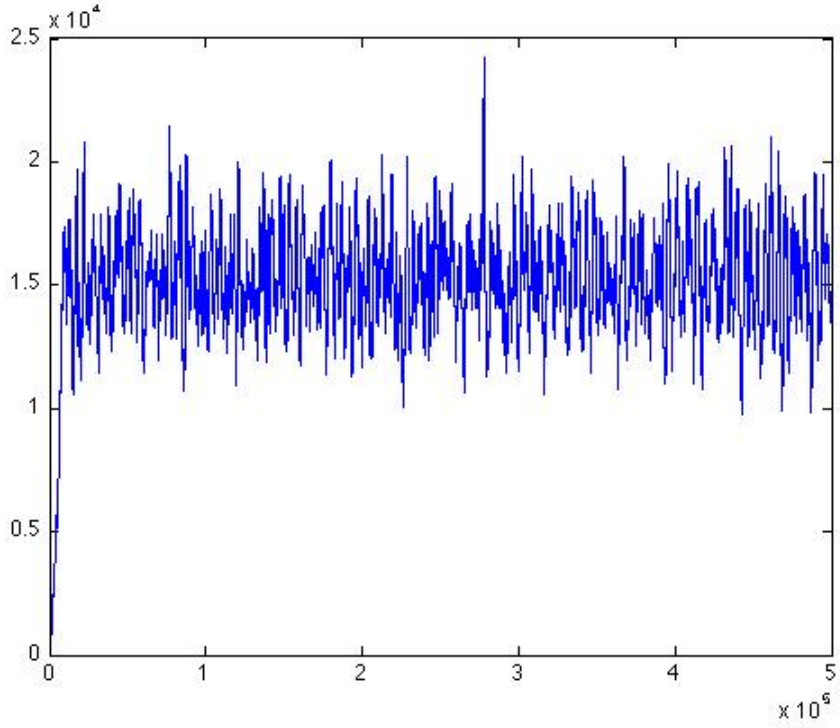
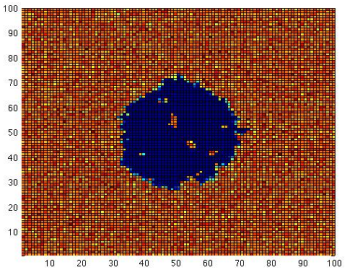
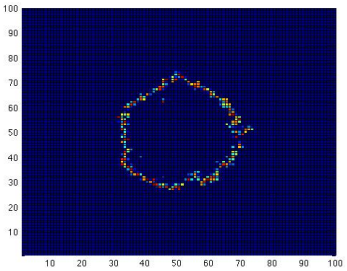


Table 5.13: Plots of the agent population in time for $T = 0.11$ and no kairomone secretion. The populations exhibit long term stable co-existence, each oscillating about a stable long term average. Mean number of AC is 104,170 (87%), mean number of AD is 15,131 (13%). Standard deviations in the AC and AD populations are 30,667 and 2,327 respectively.

With Indiscriminate Kairomone Secretion $(\nu = 1)$

The wave of invading AD travels outwards slightly faster than in the non-kairomone case. The remaining AC population is distributed much more unevenly, with a smaller number of colonies of significantly larger spatial extent. Both populations are more volatile than the without kairomone case. At times when the AD population is particularly low, the AC population quickly expands to fill almost the entire grid before encountering a small peripheral AD colony that then rapidly reduces the AC back to much lower levels. In terms of the AD agents, the grid is much more sparsely populated, with very much fewer colonies, though they tend to form much longer linear structures whose movement resembles that of spiral wavefronts. The mean population of the AC was found to be 136,400 individuals, which is approximately 31% higher than in the above zero kairomone case and represents 95.7% of the present population. Thus kairomone would seem to favour the AC, allowing them to locate one another more efficiently and thereby benefit from their mutual interaction. The mean population level of the AD only 5,922 which is some three times lower than the AD population in a zero kairomone environment and only 4.2% of the total population. Cearly in this case kairomone secretion is to the benefit of the AC, though it also makes the entire dynamics more volatile.

Always Cooperate	Always Defect
	
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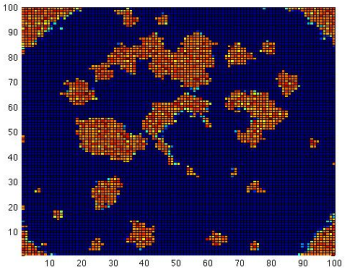	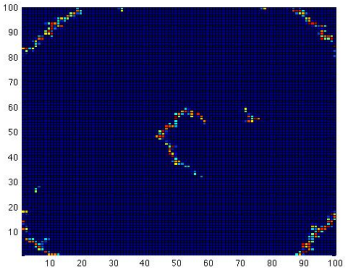
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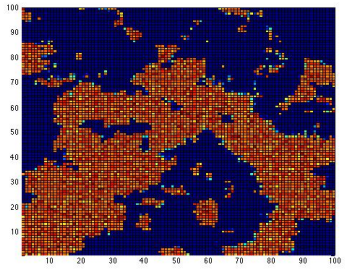	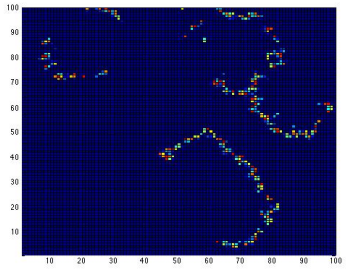
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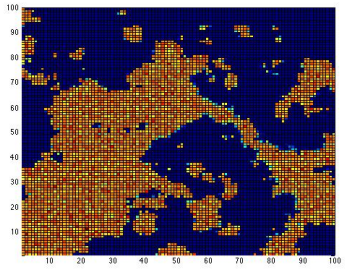	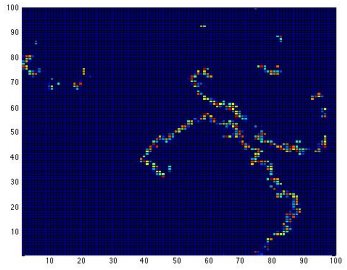
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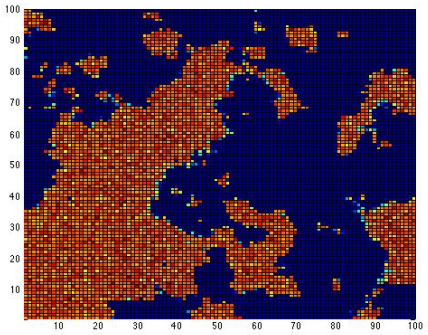
Always Cooperate



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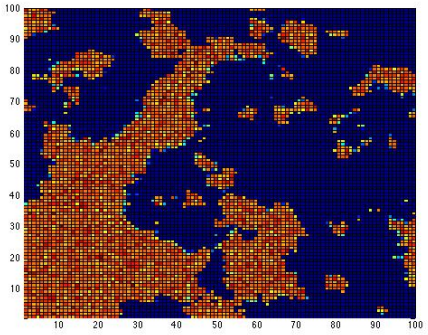

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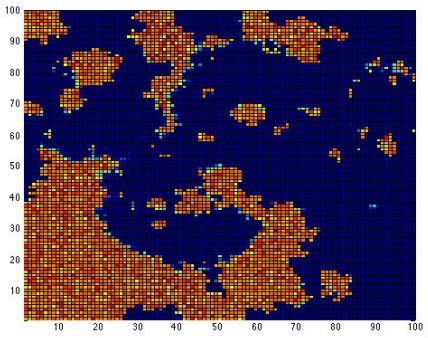

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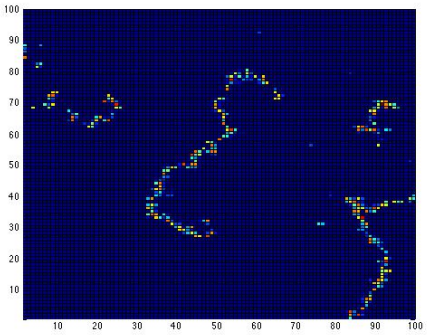
Always Defect



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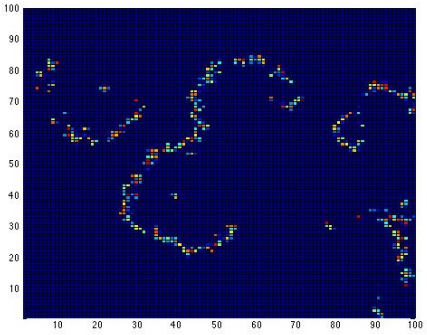

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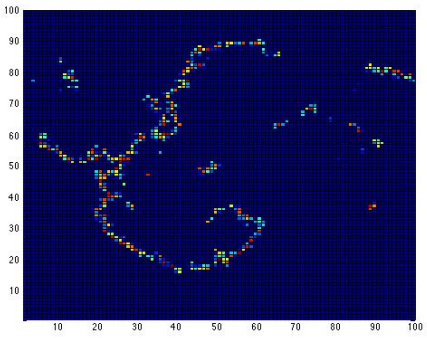

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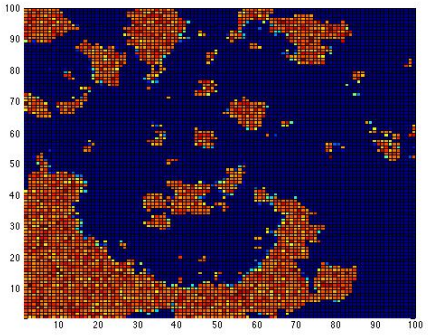
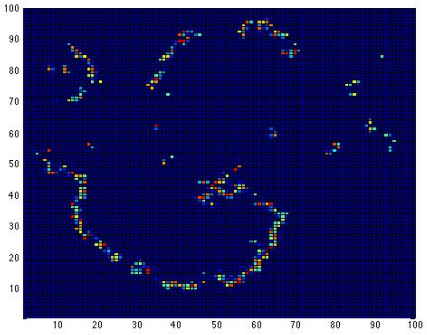
Always Cooperate	Always Defect
	
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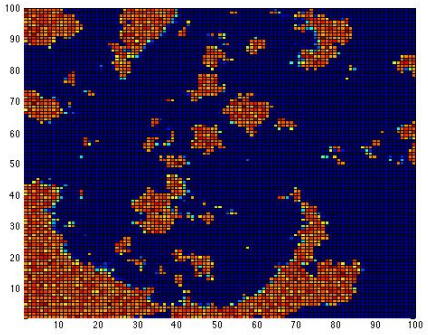	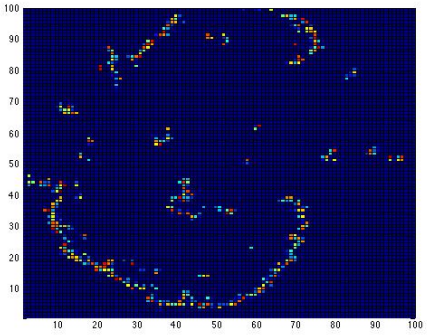
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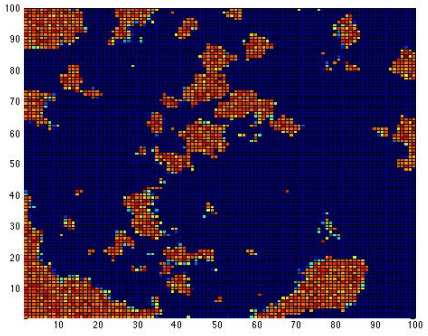
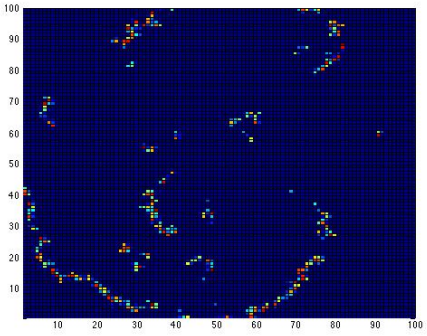
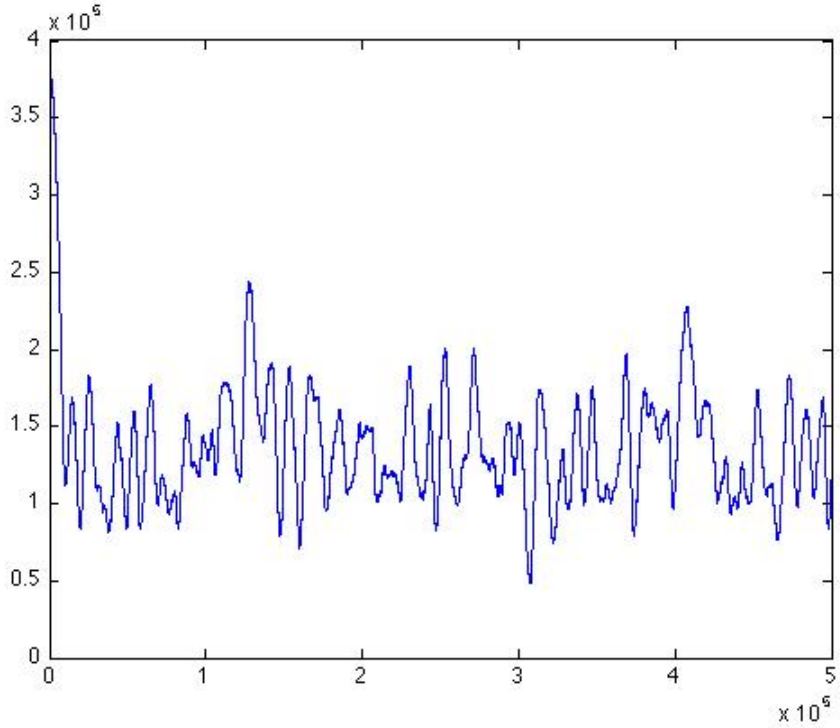
	
t = 321,000	t = 321,000

Table 5.14: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC. AD wavefront moves swiftly across the grid. The remaining residual populations of AC recover quickly and are highly clumped. The AD population persists at a very low level as filamentary wavefronts that are often seen to advance in a spiral fashion.

Always Cooperate



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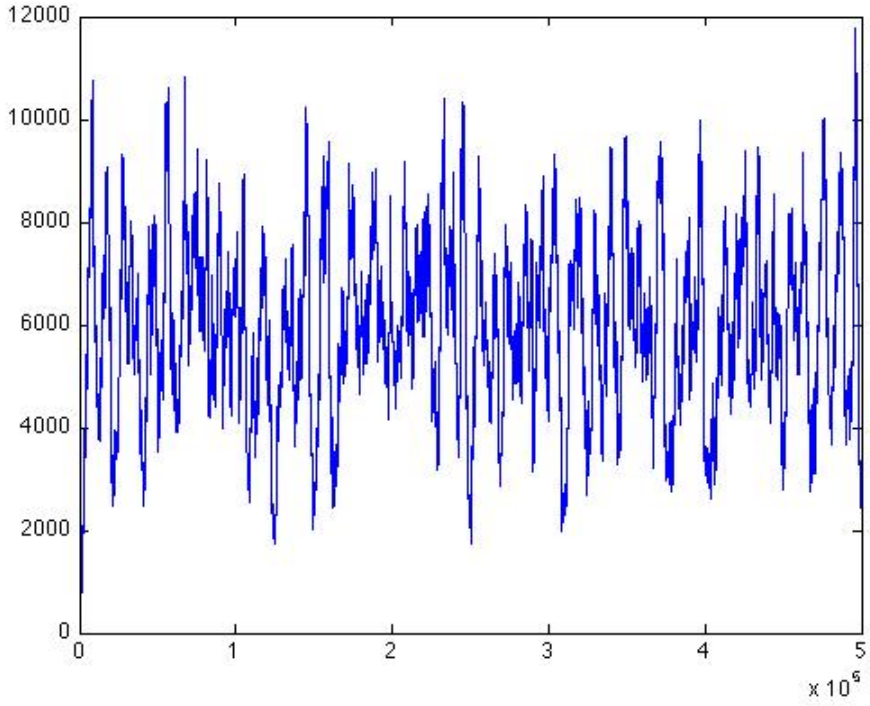


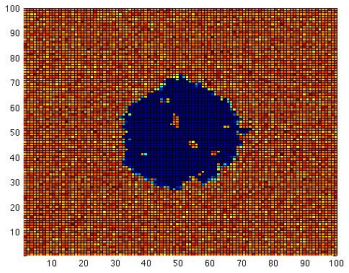
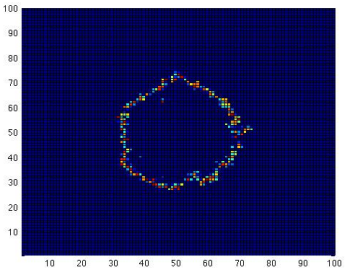
Table 5.15: Plots of the agent population in time. Populations are volatile and the AD persist at a relatively low level. AC population time average is 136,400 (95.8%) while the number of AD is merely 4.2% at 5,922. Standard deviations are 39,371 and 1,704 respectively.

With Kairomone Secretion for AC only $(\nu_{AC} = 1)$

For this regime, the populations are on the very edge of mutual coexistence. Any further increase in the payoff of Defect against Cooperate, i.e. in T, leads to the extinction of the AD agents.

The initial AD wavefront moves very fast through the background AC population. The AC population is extremely clumpy and sometimes occupies large areas of the grid. The AD population, although small, for well defined filamentary wavefronts that tend to advance in a spiral fashion. These wave fronts are very destructive when they meet an AC population. These wavefronts also tend to annihilate each other when they meet. On several occasions the AD approach extinction with populations at very low levels.

The AC population here is the highest in the three cases considered, at 149,510 individuals it is approximately 43% higher than the zero kairomone case and some 10% higher than the indiscriminate kairomone case. Likewise the AD are at their lowest mean level, being only 5,283 individuals which is around three times less than the AD mean population in a zero kairomone environment, and slightly lower than the mean number of AD in an indiscriminate kairomone secretion scenario. The fluctuations about the mean are substantial, representing a less stable state of coexistence than the above two cases.

Always Cooperate	Always Defect
	
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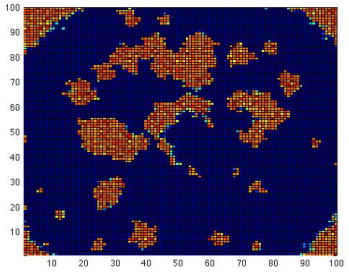	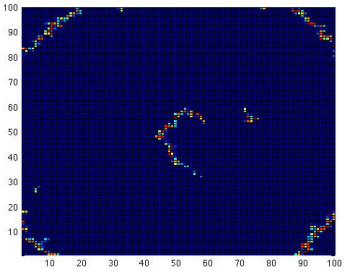
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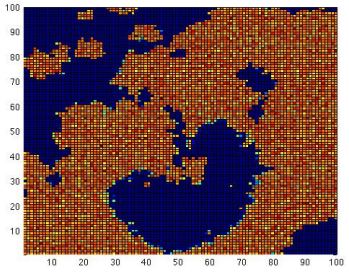	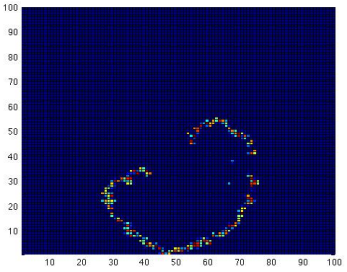
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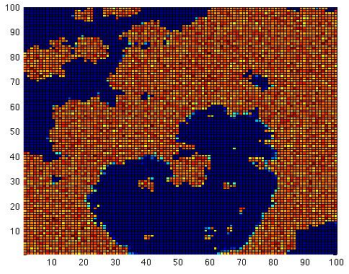	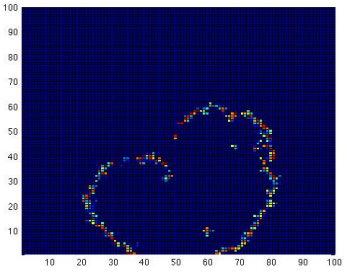
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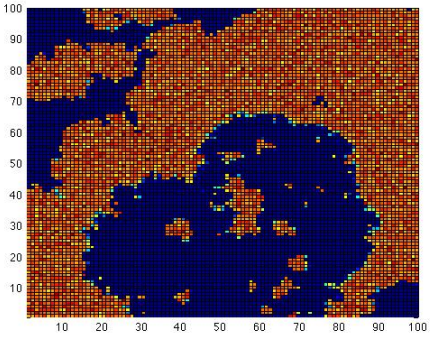
Always Cooperate



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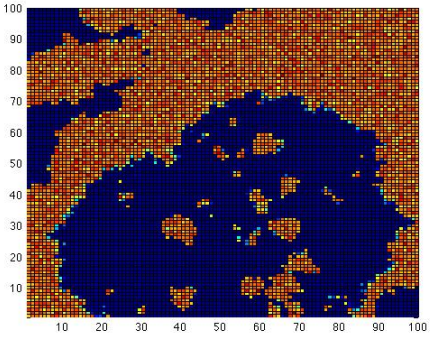

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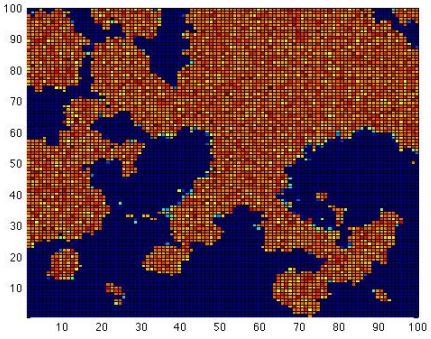

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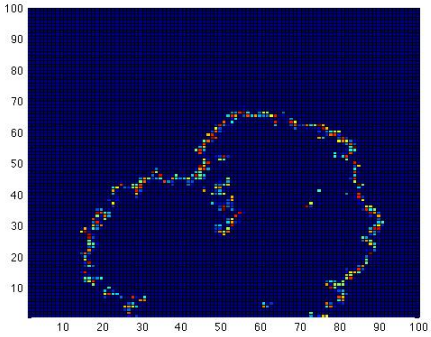
Always Defect



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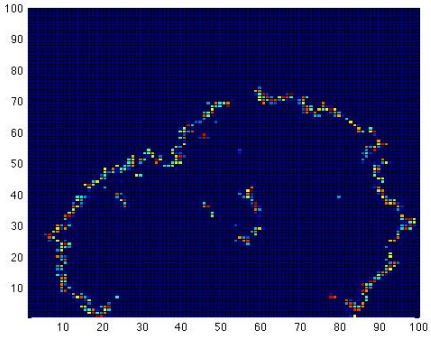

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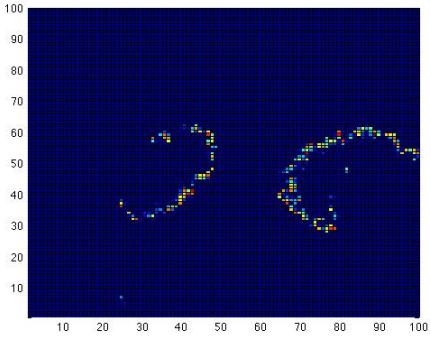

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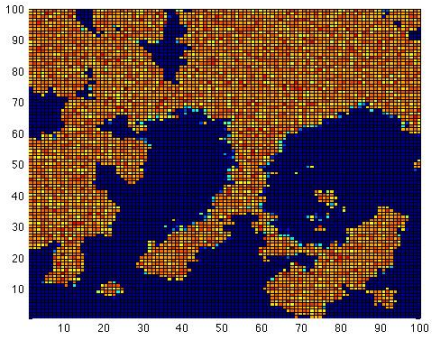
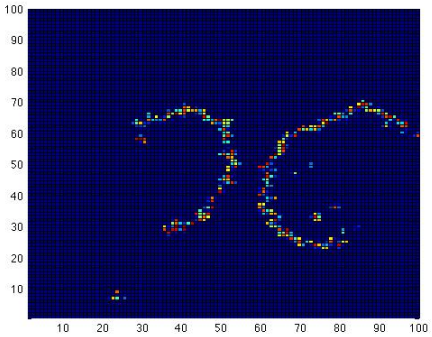
Always Cooperate	Always Defect
	
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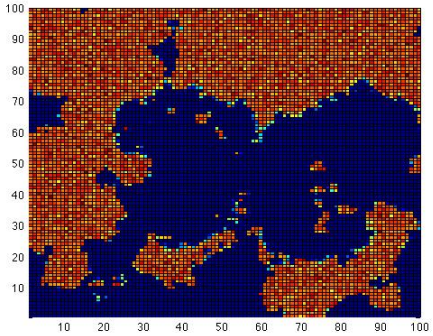	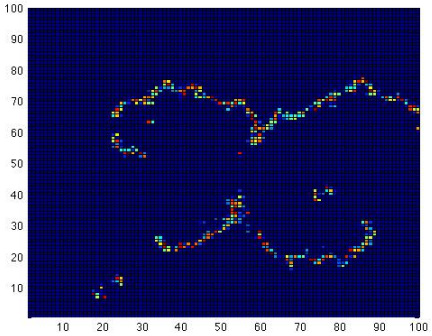
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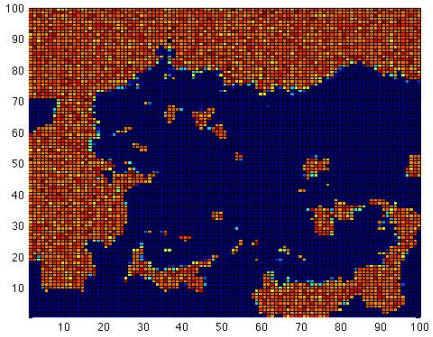
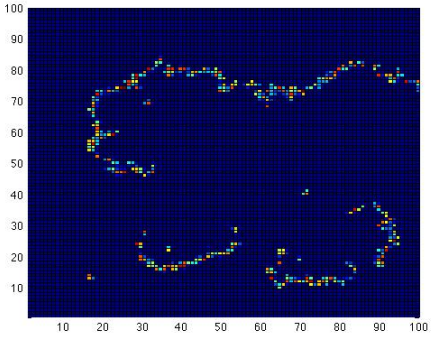
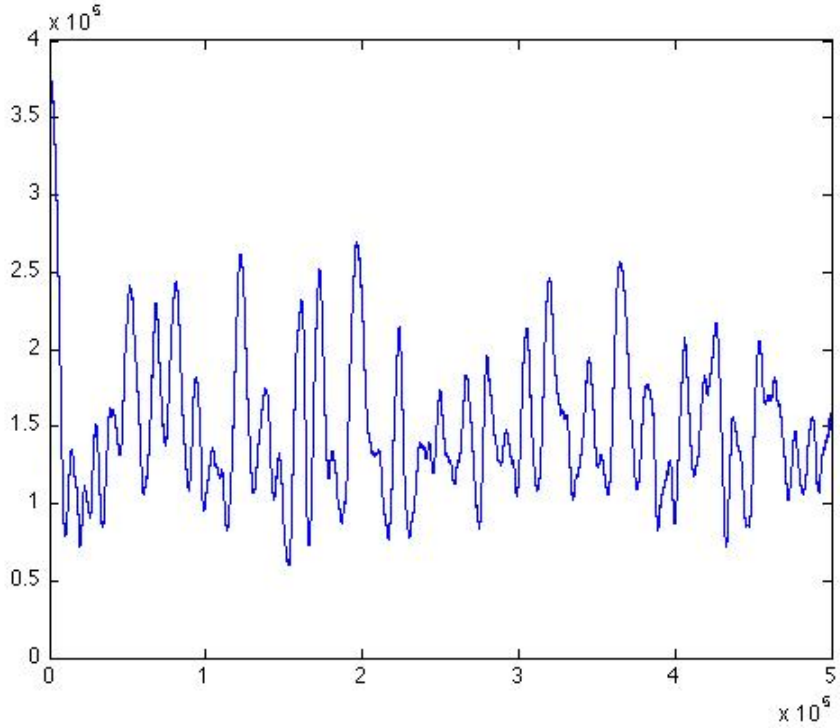
	
t = 429,000	t = 429,000

Table 5.16: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one AD at the centre of a grid surrounded by a random distribution of 49,999 AC. AD wavefront moves swiftly across the grid. The remaining residual populations of AC recover quickly and are highly clumped. The AD population persists at a very low level as filamentary wavefronts that are often seen to advance in a spiral fashion.

Always Cooperate



Always Defect

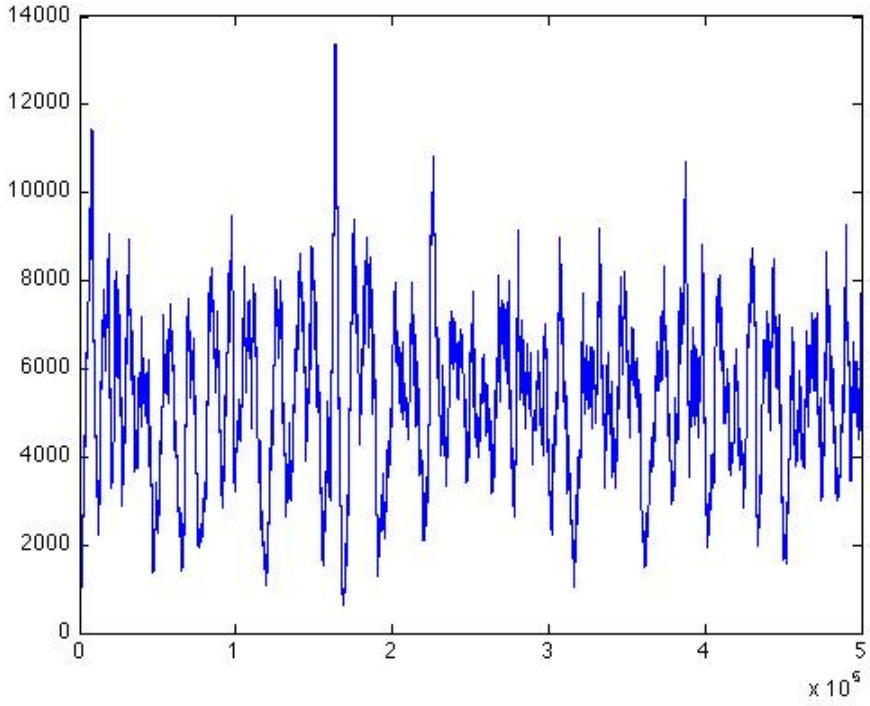


Table 5.17: Plots of the agent population in time. Populations are volatile and the AD persist at a relatively low level. AC population time average is 149,510 (97%) while the number of AD is merely 3% at 5,283. Standard deviations are 47,334 and 1,827 respectively.

The Effect of Kairomone Secretion

In all cases the secretion of kairomone has a detrimental effect on the AD, with the targeted secretion by AD only correlated with the lowest AC populations. For the AC, kairomone secretion was on the whole beneficial, especially when indiscriminate. However, the numbers of AD declined rapidly in the presence of kairomone, both in absolute terms and as a percentage of the total population of the grid. Kairomone acted to create fewer but larger population centres for AC. This in turn led to more empty grid-space, and it is probably in this way that the AD numbers were most affected. The fact that targeted kairomone secretion by the AC only was most detrimental to the AD was surprising. Initially it was thought that this mechanism should prevent the AD being attracted to one another and allow them to more easily locate the AC. However, it seems that the dominant effect in this case was that kairomone secretion by the AD acted to attract local concentrations of AC. Taking away from the AD the ability to manufacture kairomone meant that they were no longer actively attractive to the AC, and the attraction of the AC for the AD was an effect that outweighed the negative impact of AD-AD kairomone mediated attraction.

Table 5.18: Comparison of Simulation Results for Case $T = 0.07$, $R = 0.02$

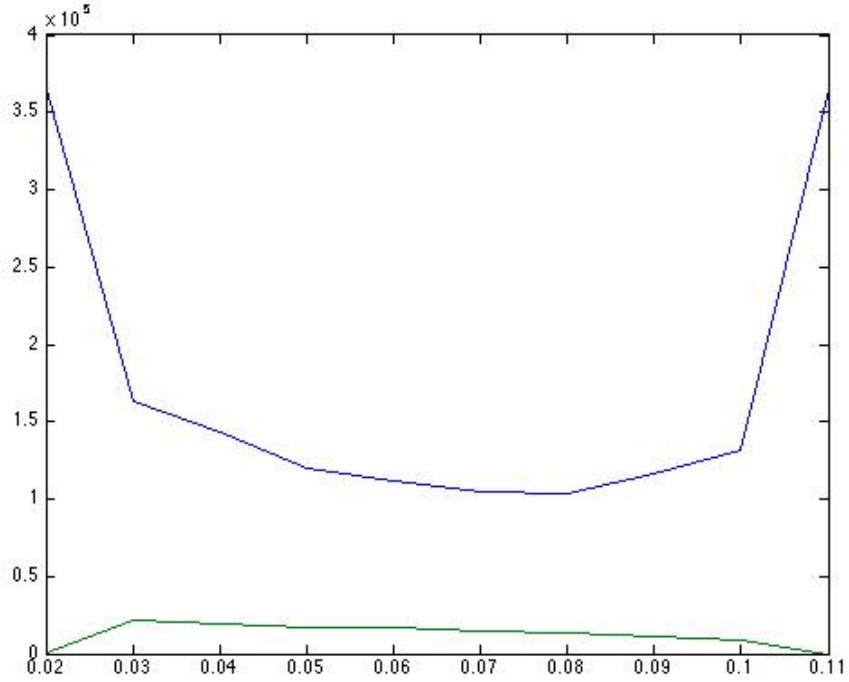
Case	Kairomone (v)	AC Mean	AD Mean	Comment
1	0	104,170 (87.3%)	15,131 (12.7%)	Coexistence
2	1	136,400 (95.7%)	5,922 (4.2%)	Coexistence
3	1 for AC only	149,510 (96.7%)	5,283 (3.2%)	Coexistence

Varying the Payoff Matrix Parameter T

Simulations were run for different values of T, which is to say for different values of the degree of advantage of an AD over and AC in an AD-AC contest. The results are qualitatively the same as in the synchronous case. The below graphs in table 5.19 cover

the case of a zero kairomone environment. The range of values for which coexistence is possible extends from $T = 0.03$ to $T = 0.10$. For values of T above this range the AD become extinct. For $T < 0.2$ the payoff matrix will cease define a Prisoners' Dilemma, and so such values of T will not be considered in this section. Anyhow, in this regime such values lead to extinction of the "AD" agents. Note the low level of the AD population when compared to the synchronous case.

Population as a Function of T



Percentage Population Composition as a Function of T

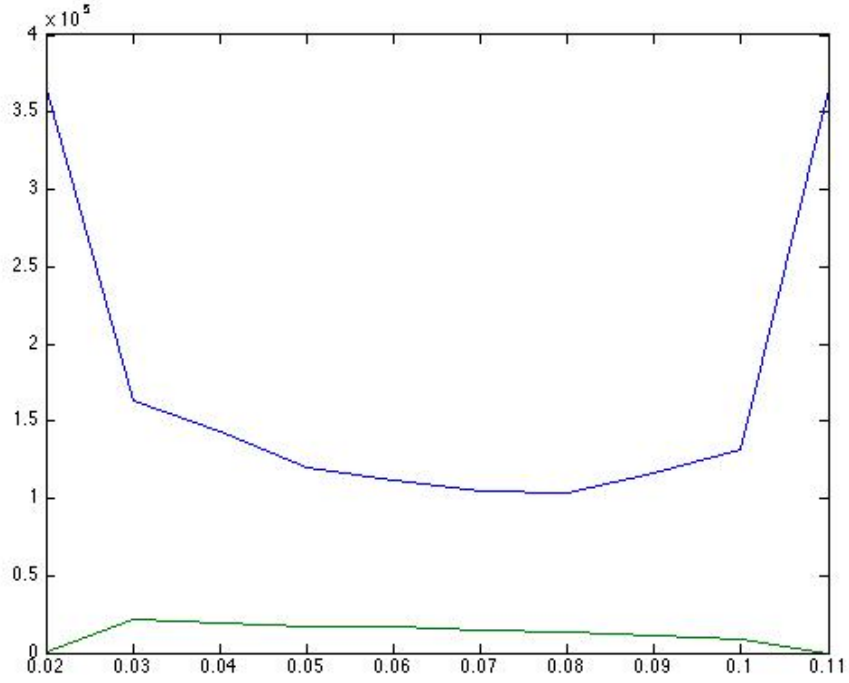


Table 5.19: The case of no kairomone secretion. As T increases from its minimum possible value of 0.02, the AC population falls in response to a stable invasion by a minority of AD. As T increases further the AD become too virulent for long term viability.

5.3 Comparison between Synchronous and Non-Synchronous Dynamics

On comparing like simulations in which the only difference was whether or not generations were synchronous or non synchronous, it is clear that the AC population was substantially higher in the non synchronous cases. Without kairomone the AC population mean was 104,170 compared to a synchronous mean of 82,141. The increase is 26.8%, with similar figures in the two kairomone secreting cases. The effect on the AD was the opposite, with non synchronous AD populations significantly lower than when generations were synchronous. By means of comparison, we note that when there was no kairomone present, the non-synchronous AD population mean was 62.5% of its synchronous value, at 15,131 compared with 24,011. Comparison of the population plots shows that the size of the variations in proportion to the mean level, was higher for the non-synchronous case. Thus coexisting populations were found to be more stable for synchronous generation than for non synchronous dynamics

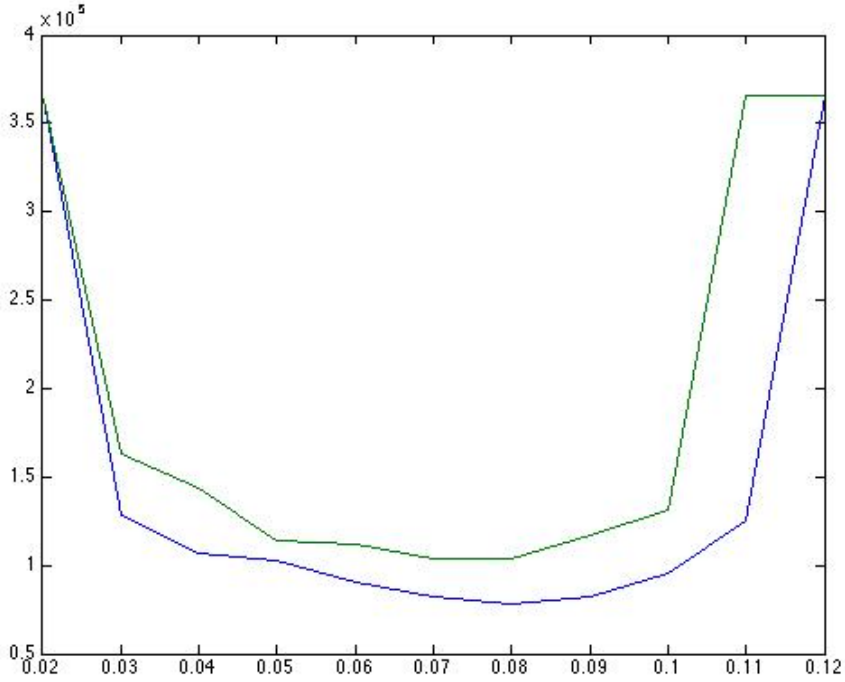
In both cases the effect of kairomone secretion was the same, which is to say that it was on the whole beneficial to AC numbers and detrimental to the AD. The effects on both populations being most pronounced in the non-synchronous case.

The below plots compare the population levels for both synchronous and non synchronous generation dynamics in the case of a zero kairomone environment as a function of the payoff parameter T. For any given value of T the AC population is generally higher in the non-synchronous case. The opposite is true for the AD, as for any given value of T the synchronous AD population exceeds the non-synchronous AD population.

Thus it would seem that allowing the generation dynamics to become non synchronous consistently acts to the benefit of the AC, or to the detriment of the AD. The effect

is both in terms of lower AD populations and also a reduced range of T for which mutual coexistence of both strategy types is possible. The same is true of kairomone secretion, which also seems detrimental to the AD. Thus for the defectors the worst of all possible worlds will be the case of non-synchronous generations in a kairomone secreting environment.

AC Population as a Function of T for both Synchronous and non-Synchronous Generations



AD Population as a Function of T for both Synchronous and non-Synchronous Generations

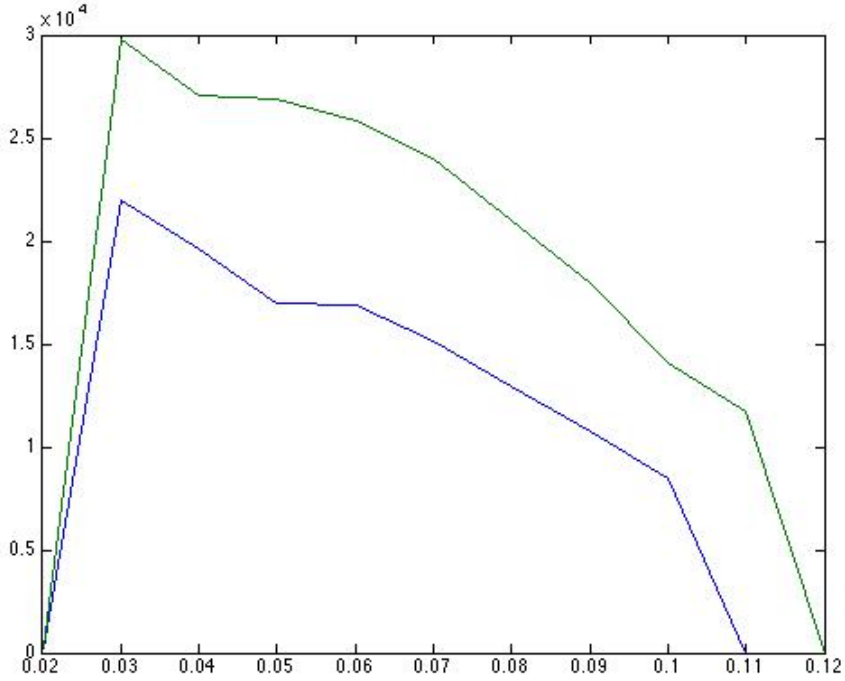


Table 5.20: Plots of population as a function of T for a zero kairomone environment, comparing synchronous and non synchronous generation results. The top line of the top graph represents population of AC in the non-synchronous case. The top line in the bottom graph represents the population of AD in the synchronous case.

5.4 Mutations

The computer code that implements these simulations has been designed to allow mutation in kairomone productivity, kairomone sensitivity, and the probability of defection. There are many scenarios that might be considered with different starting configurations and different mutation probabilities and mutation amounts for the given traits.

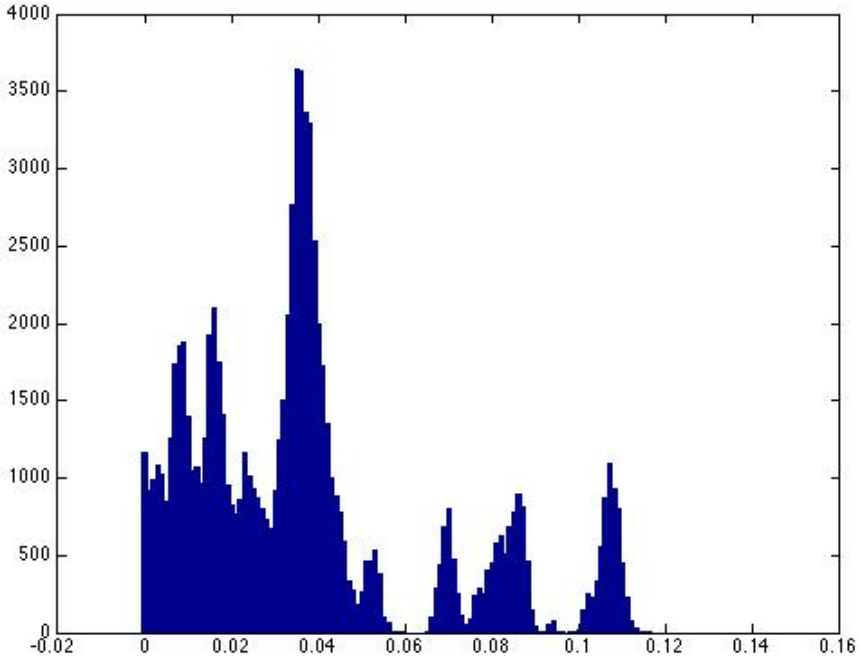
Mutation in the Production of Kairomone

We consider our standard payoff matrix parameters with $T = 0.07$. We start with both agents not secreting kairomone. We allow both strategy types to mutate their values for kairomone productivity in the same way. The mutation method implemented is as follows: there is a relatively large probability of 0.01 for a relatively small increment in kairomone productivity of 0.001. There is an additional probability of 0.0001 for a relatively large mutation in kairomone productivity of 0.01. There is an equal probability that the mutation will either in crease or decrease the kairomone productivity. The system is then allowed to run for an extended period of two million time steps, corresponding to twenty thousand generations. The final distribution of kairomone production coefficients are then plotted.

At the end of the simulation the kairomone production coefficients for the AC were distributed with mean 0.038 and standard deviation 0.0285. The modal value was more of less equal to the mean. There was a substantial fraction of the population remaining at kairomone productivity of zero, and the highest value attained was 0.115. The values for the AD were distributed about a mean of 0.0284 with a standard deviation of 0.0207.

During the course of the simulation there seemed to be a consistent evolution towards higher values of the kairomone productivity for both agent types. There was no detectable alteration in the average population values, and both populations appeared to fluctuate about stable long term averages, being 78,222 (76%) individuals for the AC and 24,294 (24%) for the AD. The population plots as a function of time are given after the kairomone distribution plots below.

Distribution of Kairomone Production Coefficients for AC



Distribution of Kairomone Production Coefficients for AD

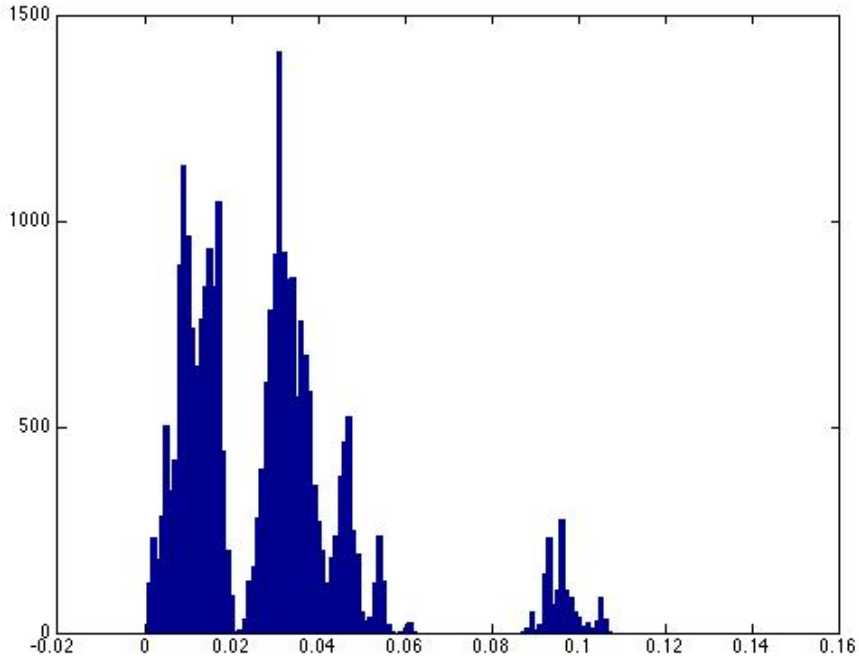
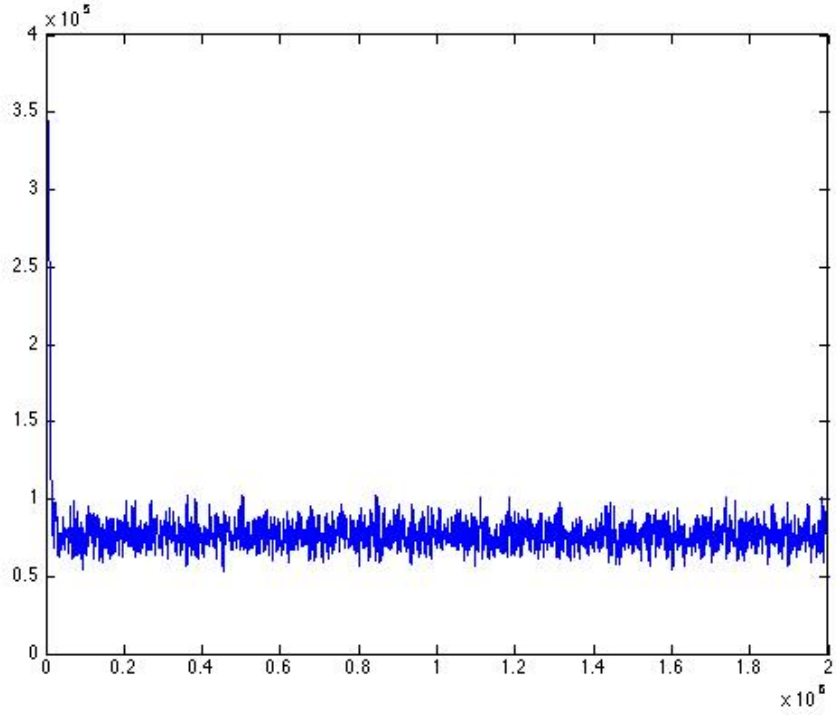


Table 5.21: These plots show the distribution of the kairomone production coefficients for AC and AD agents after a period of two million time steps starting from a configuration in which all such coefficients were set to zero.

Always Cooperate



Always Defect

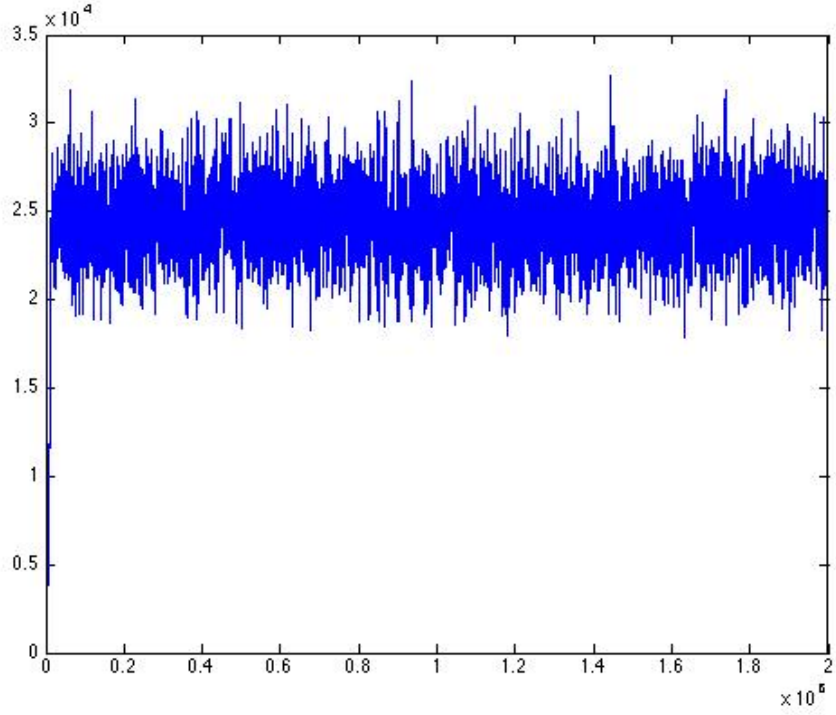


Table 5.22: The AD and AC populations displayed remarkable stability over the two million time steps for this simulation, despite the mutation in the value of the kairomone secretion. Mean number of AC was 78,222 with a standard deviation of 19,921. AD were distributed about a mean in time of 24,294 with a standard deviation of 2,446.

A shorter simulation was run in which mutation was run in which only the AC were allowed to mutate their kairomone production, and in which the AD were sensitive to kairomone but did not produce it themselves. The result was again a small increase in the average level of kairomone production among the AC. By the end of 1,200,000 time steps the AC kairomone production was distributed about a mean of 0.0597 with a standard deviation of 0.0571. A plot is given below.

More simulations are required in this area, with longer simulation times. It will be interesting to then note whether population averages will vary in the long term as a result of the changing kairomone levels in the environment.

Distribution of Kairomone Production Coefficient for AC

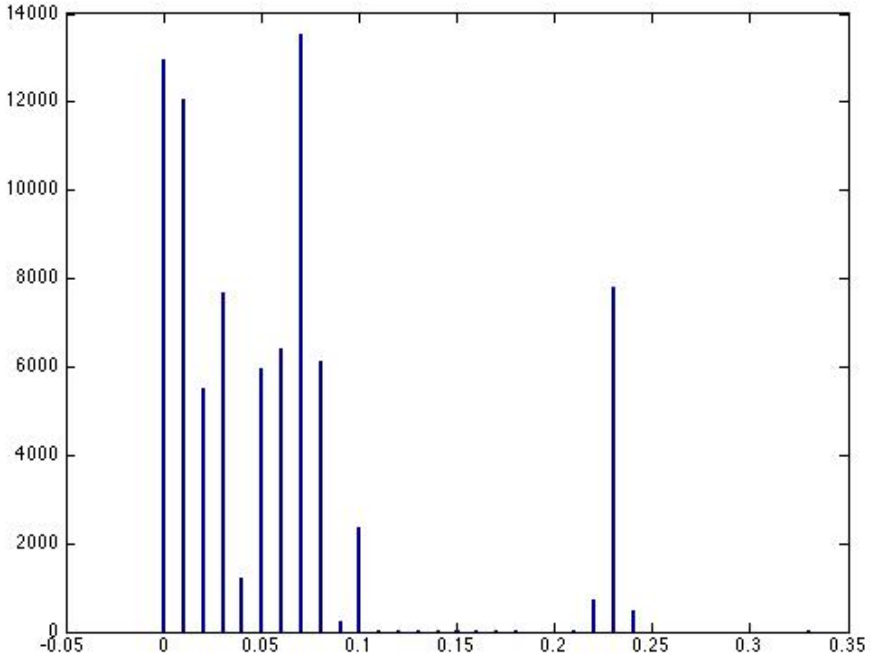


Table 5.23: In this simulation only AC were allowed to mutate their kairomone productivity coefficient. The starting value was zero. AD did not produce kairomone but remained sensitive to it. By simulations end at t = 1,200,000 the mean kairomone production coefficient was 0.097 with a standard deviation of 0.0571.

Mutation in the Probability of Defection

In this section we investigate the effect of mutations. We start with a purse strategy set of cooperators. We then allow mutation in the probability of defection at any given interaction. This allow an initially AC population to mutate into a mixed population. Mutation occurs at reproduction which occurs at the end of an agents lifetime (synchronous generations).

Simulation 1

In the following simulation we briefly consider the implications allowing the strategies themselves to mutate. We achieve this by considering mixed strategies, and then allowing the probabilities with which certain strategies are played to mutate. In this first example we start with a population composed entirely of cooperators. Initially we set the probability of defection equal to zero, but we allow this probability to change via mutation at reproduction. The probability of a mutation is set to be 0.001 (one in a thousand), and the mutation amount (the allowed change in the probability of defect per a mutation) is set at 0.01. There is no kairomone production in this simulation. In order to increase the selective pressure to mutate we consider a high value for T of 0.11 and a relatively low value for R of 0.01. Thus the payoff matrix for this example is:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 0.01 & 0 \\ 0.11 & 0.001 \end{pmatrix} \end{array} \tag{5.2}$$

Due to time constraints the simulation was run for a mere 120,000 time steps. But in that time there was a notable change in the population strategies.

Below in table 5.24 is a plot detailing the probability of defect at the simulation end. By the end of the simulation the mean value for the probability of defection was 0.2887 with a standard deviation of 0.0143. There was thus a move toward a significant probability of defection in a short period of time. More simulations of longer duration are required to investigate this issue satisfactorily.

Distribution of the Probability of Defection

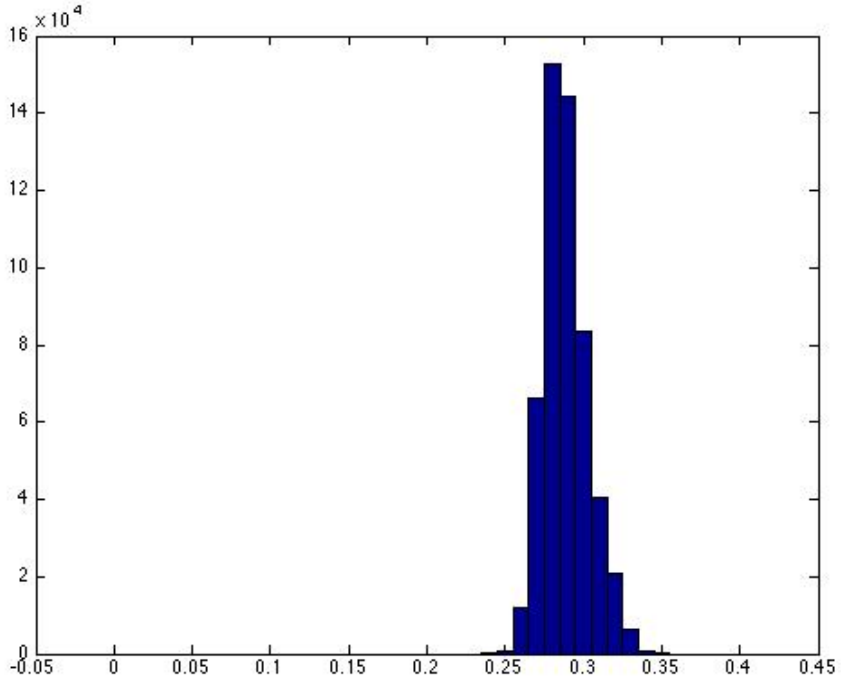


Table 5.24: In this simulation we consider an initial population of AC individuals and allow mutation in the probability of defection from zero in increments of 0.01. Simulation ended at t = 120,000 at which time the above plot was made. The mean value for the probability of defection was 0.2887 and the standard deviation was recorded as being 0.0143

Total Population

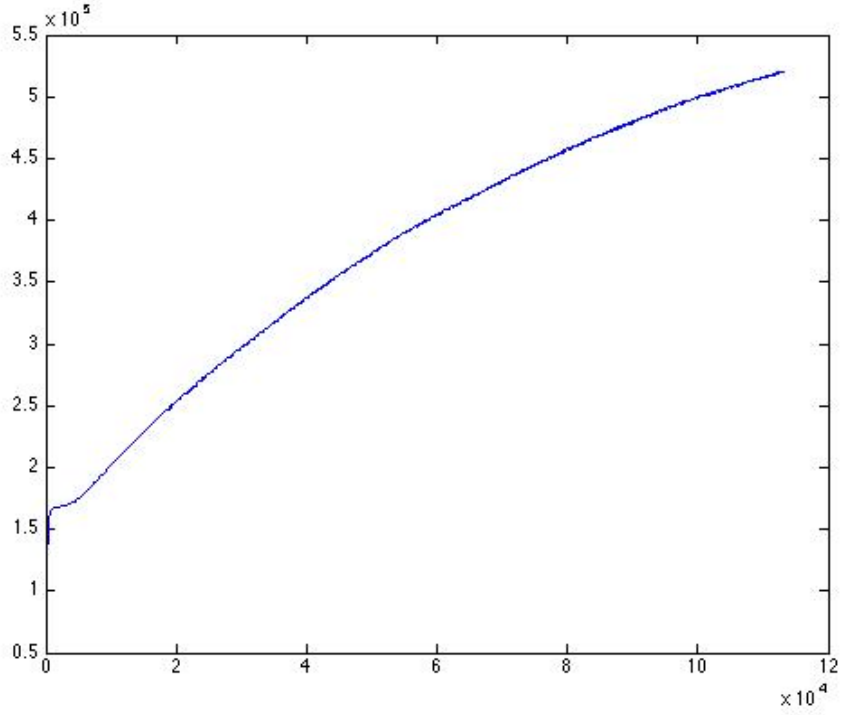


Table 5.25: The total population increased throughout the simulation.

Simulation 2

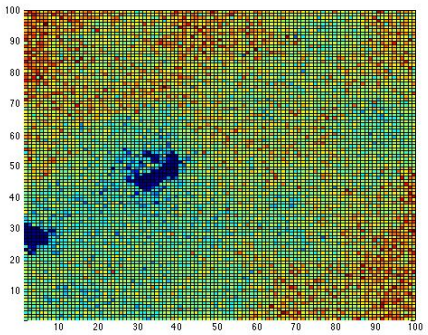
In this simulation we adopt the standard parameters for our Prisoner's Dilemma investigation, with $T = 0.07$ and $R = 0.02$. There is no kairomone secretion. We set the probability of mutation at 0.001 and set the mutation amount to be 0.01. Which is to say, at each reproduction, the probability that an offspring will differ from its parent in the probability of defection (by 0.01) will be 0.001. This simulation was allowed to run for two million time steps.

The results demonstrate a clear selection pressure to increase the probability of defection. Initially this is to the benefit of the population as a whole as the entire population increases. However, this trend is short lived and a maximum population level is achieved at approximately $t = 250,000$, or at 2,500 generations. Thereafter the population declines it mutates with a further increased probability of defection. By just after $t = 760,000$ or 7,600 generations, the population has become extinct. At each reproduction, it seems that there is an individual advantage to increasing the likelihood of defection. There seems to be a selection pressure to defect. However, globally this trend has a detrimental effect, for it means that the overall payoff gained over the population decreases as each player becomes more likely to be involved in several rounds of mutual defection. Thus the population enters a terminal decline and extinction is inevitable. This indicates a recurrence of one of the most fascinating aspects of the Prisoner's Dilemma as originally devised, which the opposition of the interests of the group to the interests of the individual. Essentially by allowing individuals the choice to become more of less cooperative, we have witnessed the break down of an initially cooperative state as the clear individual pressure is to defect to gain increased individual payoff and thereby offspring. But thereby the global accumulated payoff, and therefore the population, decreases.

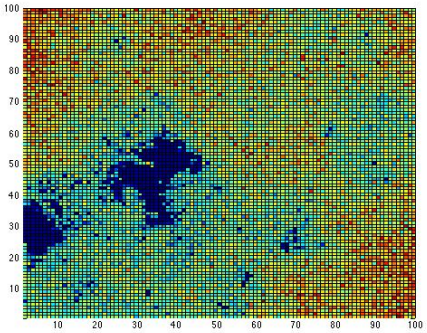
In this case the population became extinct because the defectors could not gain enough

payoff from their mutual interaction to sustain a viable population. By increasing the payoff to a defector against a defector we could allow a population of pure defectors to survive. In this case we would not see an extinction, but rather a reduced stable end state population level consistent with mutual defection.

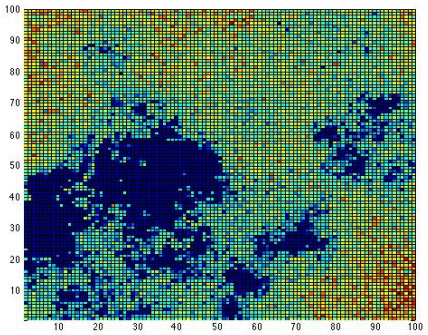
Below in table 5.26 we provide grid plots that show the final stage of this evolution, in which the population is approaching extinction. There are several concentrations of defectors that leave a wake of empty space as they expand into the less 'defective' population.



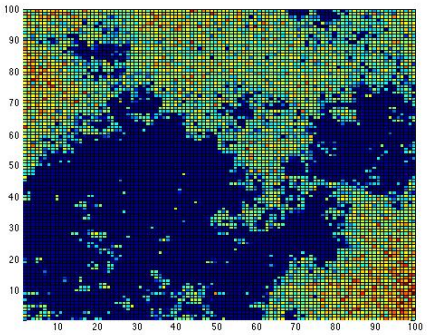
t = 316,000



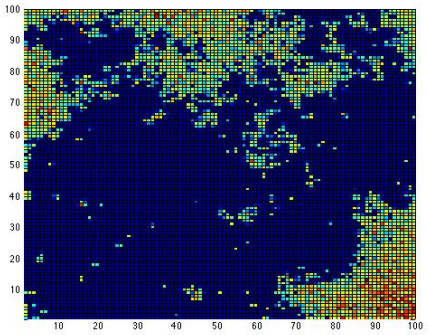
t = 316,000



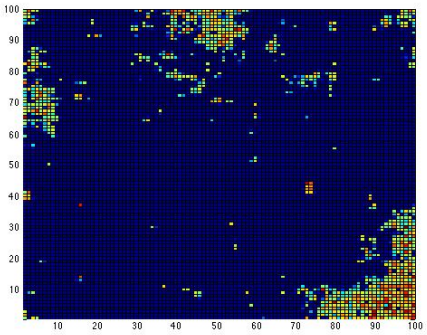
t = 317,000



t = 317,000



t = 318,000



t = 318,000

Table 5.26: Snapshots in time depicting spatial distribution of agents as the population approaches extinction as they mutate towards the strategy Always Defect.

Total Population

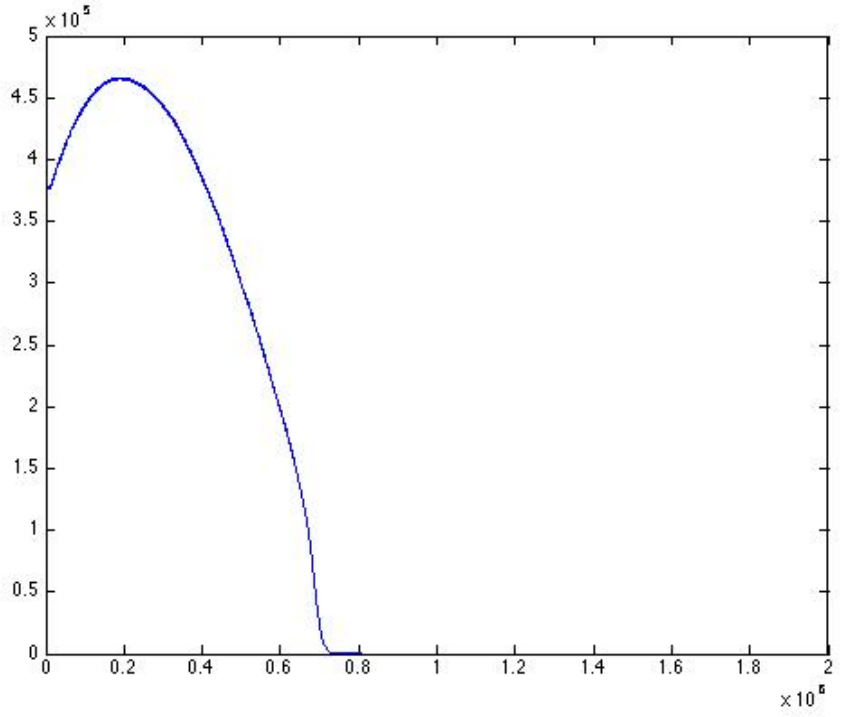


Table 5.27: As the population evolved towards increasing levels of defection, the population declined and eventually extinction resulted.

5.5 Discussion

The significant feature to note regarding the above simulations is the long term stable spatially heterogeneous oscillatory dynamics.

Co-existing stable dynamic states are found that differ from what would be expected from the traditional game theory analysis. Indeed, the notion of ESS does not strictly apply to these situations. For AD to be an ESS it would be necessary that it be the most profitable strategy in a population that is almost entirely composed of AD. Yet for our regime, although AD may survive in a population with a significant AC component, they cannot survive in isolation as a monomorphic population of AD. In this sense, such configurations are very far from the applicability of the ESS equilibrium.

Kairomone secretion seems to have a destabilising effect on these simple ecologies, with populations of AD reduced and as general rule standard deviations increased. One might regard the effect of kairomone secretion as a means by which a smaller number of parasitic agents is able to cause greater damage to a background host population and thereby cause such local destruction as to prevent its own recovery. The range of values of T (the payoff for a Defector against a Cooperator) for which a population exhibits mutual coexistence of strategies is larger for the non kairomone secreting case than in the simulations that allowed kairomone signals. In the simulations using non-synchronous generations, the range of values for T for which mutual coexistence was possible was smaller than the range in the synchronous case.

Hosts tend to survive in clusters, which are self-sustaining and indeed grow with time. The continued existence of the parasites depends on these clusters of hosts. Host clusters typically grow from a small number of survivors of a parasite wave. Hosts then rapidly increase in number to re-seed the grid on a local basis and are then culled once their cluster expands to a size sufficient to overlap with another passing parasite

population.

The fact that the non-integer part of the payoff is discarded implies that strategies with a small payoff score are disproportionately underrepresented in subsequent populations compared with a classical analysis. This is also a feature of the Nowak and May cellular automata models.

Mutual coexistence does not of course obtain for all parameter ranges. For example, in the Prisoners Dilemma, setting $T = 0.12$, $R = 0.01$ consistently results in the eventual collapse of the AD population.

Although we have considered what is effectively an iterated game structure, with agents playing many rounds of the game in a single lifetime, we have not considered complicated or conditional strategies. Rather interactions consist of a series of one-shot games. We have found that cooperation persists without the need for conditional strategies of any kind. Likewise, cooperation persists without the need for negotiation or collective behaviours that are invoked by some social science models. In terms of the host parasite paradigm, we observe the persistence of hosts in a spatial environment without the need for immunity. Unlike [56], we do not consider tags whereby players might recognise another as in some way similar to itself, neither are our agents capable of identifying the strategy of their opponent before interaction.

In some simulations, in which the payoff to Always Defect was close to the limiting value for virulent extinction, spiral wave type structures were observed. The archetypal spiral wave phenomena in nature is that exhibited by the B-Z reaction, [45]. Spiral wave features in models of host-parasitoid systems have been reported in [133], [134], where the authors consider a system based on a cellular automaton executing a Nicholson-Bailey type interactions. A similar model in continuous space and time was investigated in [135]. In Rock Paper Scissors spiral waves were reported by [23] and [112] from a stochastic PDE viewpoint. In agreement with the discussion in [149],

we note that the simulations in which spiral waves appear are characterised by more obviously oscillatory temporal behaviour of the population level.

Chapter 6

Simulation Results for the Hawk Dove Game

The Hawk Dove game was the first to be considered by the founders of evolutionary game theory in their first paper of the subject. [14].

Spatial aspects of the Hawk-Dove game for the cellular automata approach were mentioned passing in [21], [22] but not elaborated upon. Spatial effects in this game were more fully discussed in [84]. The key results in these papers is again that embedding the game theory interaction into some spatial structure leads to results that are qualitatively different from those obtained from classical evolutionary game theory. Specifically in structured populations cooperative strategies (such as Dove) can build clusters in which the benefits of mutual cooperation can outweigh losses against external defectors. The authors also proceed to consider other strategies in the Hawk-dove game, such a the 'retaliator', which we shall not do. In [94] the author considers the hawk-dove game on a lattice and remarks that "Compared to mean field calculations, spatial extension generally favours the Hawk strategy. Consequently, in spatially structured populations, we would expect to observe more frequent escalations of conflicts

than predicted by mean field theory".

The Hawk dove game on various spatial networks was analysed in [91], where is was reported that the abundance of Doves depends crucially upon the network structure as well as on the ratio V/C.

In all these approaches, although there is a spatial distribution of agents, there is no motion as such. After on round of the game a cell adjusts its strategy to follow the most successful in its immediate environs. Whether this is colonisation by the successful individual or just imitation of his strategy by previous interlocutors is largely here a matter of interpretation.

Our approach shall differ in that firstly our individual agents genuinely reproduce offspring that follow the same strategy as themselves. The reproduction of strategies cannot be interpreted as, or confounded with, imitation dynamics. Further, space is perhaps more realistically rendered in our approach, for it is possible to have concentrations of agents in some regions and hence a larger number of interaction on average than in other parts of the grid. Indeed we do not disallow the possibility, frequently realised, that parts of the grid my be totally empty. In this way our system has some similarities to models used to study disease epidemics in which population density is an important factor in pathogen propagation. We also allow explicit motion of individuals via a random walk process, which may or may not be guided by a kairomone signal.

The generic Hawk Dove game payoff matrix is as follows:

$$\begin{array}{c} \\ H \\ D \end{array} \begin{array}{c} \begin{array}{cc} H & D \end{array} \\ \begin{pmatrix} \frac{1}{2}(V-C) & V \\ 0 & \frac{V}{2} \end{pmatrix} \end{array} \tag{6.1}$$

This payoff matrix embodies an assumption, which is that in a Hawk-Hawk contest, a given Hawk individual has a 50% chance of winning a resource of value V and a 50% chance of incurring a cost C, the average payoff then being $\frac{1}{2}(V-C)$. This assumption is useful when considering large populations in which statistical fluctuations are expected to average out. On an individual level, however, we may not need to impose such an averaging. We may design the simulation such that in any given contest one Hawk will receive payoff V and the other will pay the cost (payoff $-C$) for losing.

In classical Game Theory the Nash equilibrium for the Hawk-Dove game depends on the relative values of V and C. For $V > C$, (when the value of the resource exceeds the cost of injury) the Nash equilibrium strategy is to play Hawk. This is also the ESS. For $V \leq C$, (when the cost of injury meets or exceeds the resource value) the (non-strict) Nash equilibrium is to play Hawk with probability V/C. This is also the ESS. We do not consider mixed strategies in this section, but for this two strategy game, it is a standard result that in a polymorphic population of pure Hawks and pure Doves, a proportion of Hawks amounting to V/C of the population is also stable [[14]].

We consider various ranges of the parameter V to examine the effect on the population dynamics. The usual starting condition will be a single Hawk at the centre of a 100 by 100 grid that is otherwise populated by a random scattering of 4,999 Doves.

6.1 Synchronous Generations

As described in Chapter four, each agent is assigned one of the two strategies Hawk H or Dove D. They move from their initial grid positions by means of a discretized PDE that includes the effect of a mediating kairomone chemical. Movement occurs at the end of each time step. Each agent may interact with a maximum of four others in any given time step. The payoff score received is recorded. Each agent lives for 100 time

steps, after which time each will reproduce, asexually producing clones with the same strategy and other member variables. The number of offspring will numerically equal the integer part of the total recorded payoff score for that agent.

We here consider how the population evolves from the given starting configuration when the payoffs are as given below:

$$\begin{array}{c} \\ H \\ D \end{array} \begin{array}{c} \begin{array}{cc} H & D \end{array} \\ \begin{pmatrix} 0.005 & 0.04 \\ 0 & 0.02 \end{pmatrix} \end{array} \tag{6.2}$$

which is to say that we set the parameters V and C to be 0.04 and 0.03 respectively.

Without Kairomone, Averaged Payoff Structure for Hawks

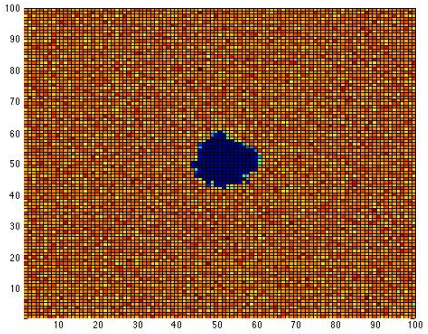
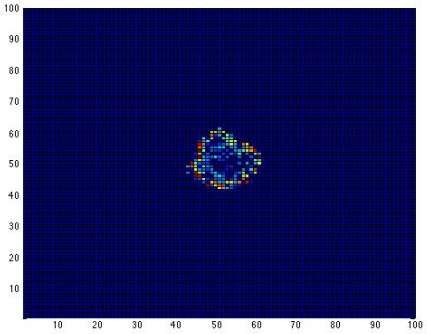
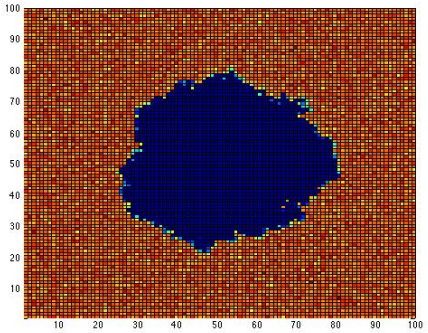
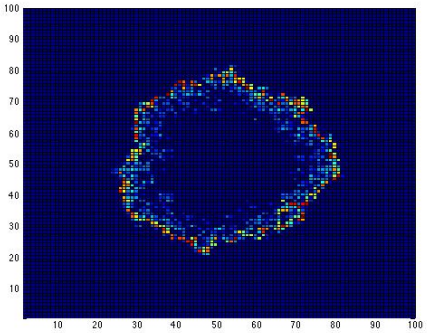
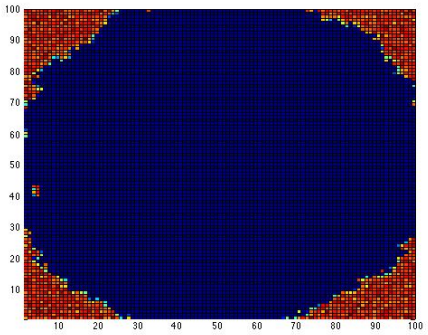
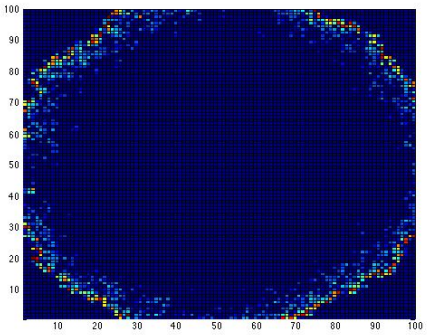
The initial single central Hawk gives rise to an expanding population of Hawks that form a circular wavefront that expands into the Dove population causing almost total devastation. A substantial number of Hawks survive in the space behind the advancing wavefront. This make the wavefront appear a little thick or spatially extended with a trailing edge in the interior region. However, in the absence of Doves, these surviving Hawks cannot sustain a viable population and within a few generations they perish. One very small population of Doves survives, in the bottom left hand corner of the grid. This is followed by a residual Hawk population. These survivors give rise to expanding fragmented wavefronts of Doves chased by Hawks that grow to repopulate the entire grid. The grid remained sparsely populated, with most grid space being empty at any one time.

After the initial invading Hawk wave front had passed, and the survivors had re populated the grid, the global behaviour became more stable. Both populations exhibited a long term stability about relatively well defined average values. This long term coexistence, which persisted for in excess of five thousand generations, was somewhat surprising given that the naive expectation was that the the Hawks, playing the ESS, should replace the Doves. The mean Dove population for the course of this simulation was 39,853 individuals. The average number of Hawks was 15,820. Thus Doves constituted some 71.6% of the population, and the Hawks 28.4%. The standard deviation in the Dove numbers was 50,321which was relatively large due to the initially high population and then the crash almost to extinction at the beginning of the simulation. Examination of the population plots however shows that thereafter the Dove population was relatively stable, with fluctuations about the mean being substantially less than the long term average population level. The standard deviation in Hawk numbers was 4,341 and the population fluctuations exhibited similar features. The major result of this simulation is that there is long term coexistence of both populations. Here this lasted for 500,000 tie steps, or 5,000 generations, before the simulation was terminated. In the context of exploring the effect of mutations, this simulation was also run for 2,000,000 time steps, or 20,000 generations. The coexistence behaviour remained stable over this extended time period.

The carrying capacity for Doves was estimated by letting the simulation run for several thousand time steps in the absence of Hawks. In this way value of was obtained for the grid Dove carrying capacity. The notion of carrying capacity was not here relevant to Hawks in isolation as for the parameter values used they were not able to sustain a viable monomorphic population.

We might venture to interpret the Hawks as being parasitic upon the Doves. The Doves, on the other hand are able to form a stable monomorphic population of around 376,000 individuals. Thus this relatively small number of Hawks had the effect of limiting the

Dove population to a stable level at approximately 10.6% of it carrying capacity.

Doves	Hawks
	
t = 3,500	t = 3,500
	
t = 10,000	t = 10,000
	
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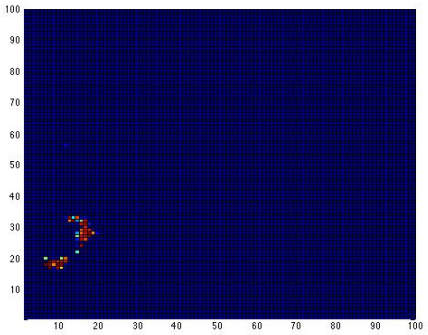
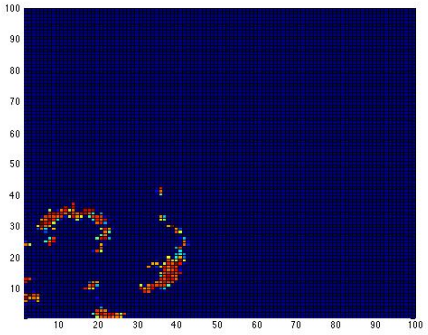
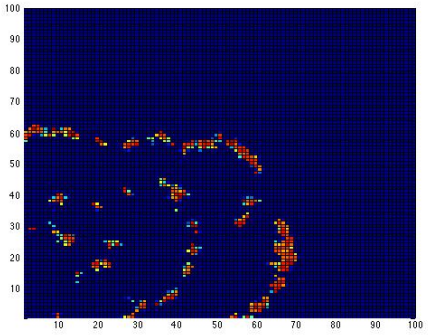
Doves



t = 30,000

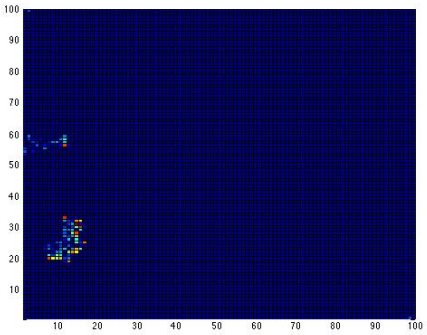


t = 40,000

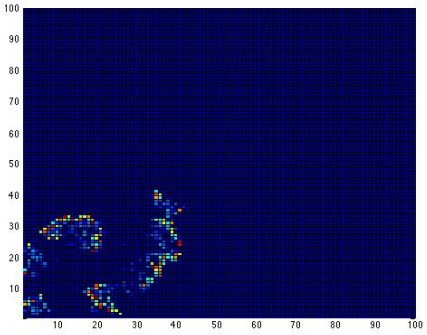


t = 50,000

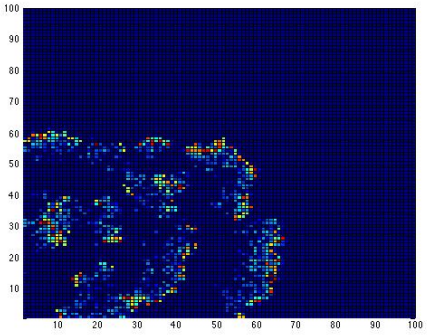
Hawks



t = 30,000



t = 40,000



t = 50,000

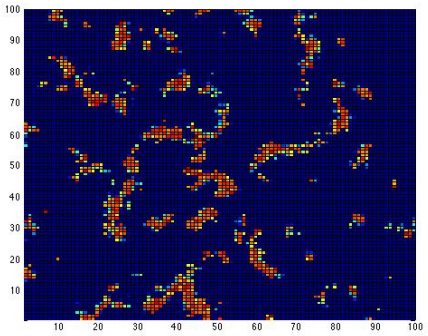
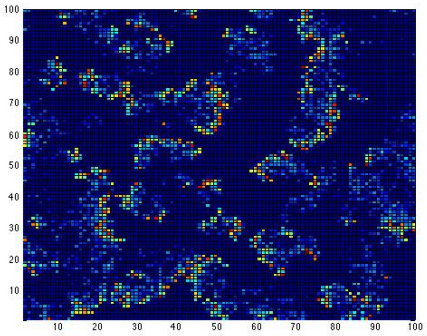
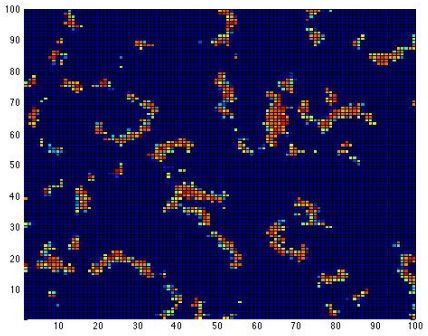
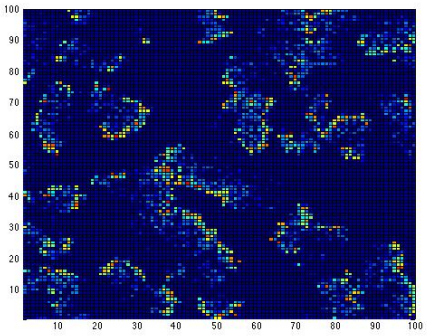
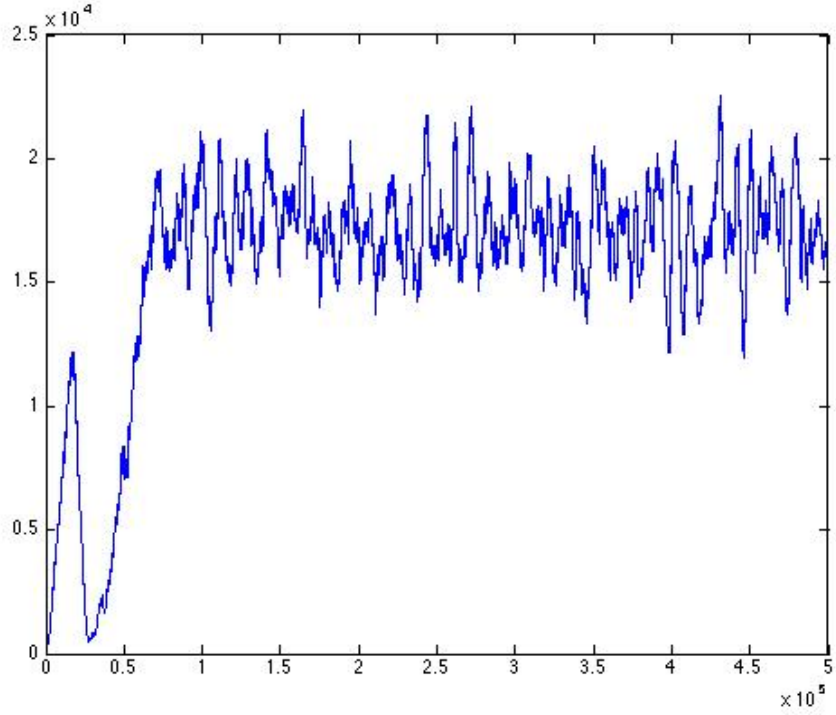
Doves	Hawks
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.1: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawk wavefront moves across the grid in a fragmented fashion. The single remaining residual population of Doves recovers to repopulate the grid. Long term coexistence is observed. The Hawk population persists at a very low level.

Hawks



Doves

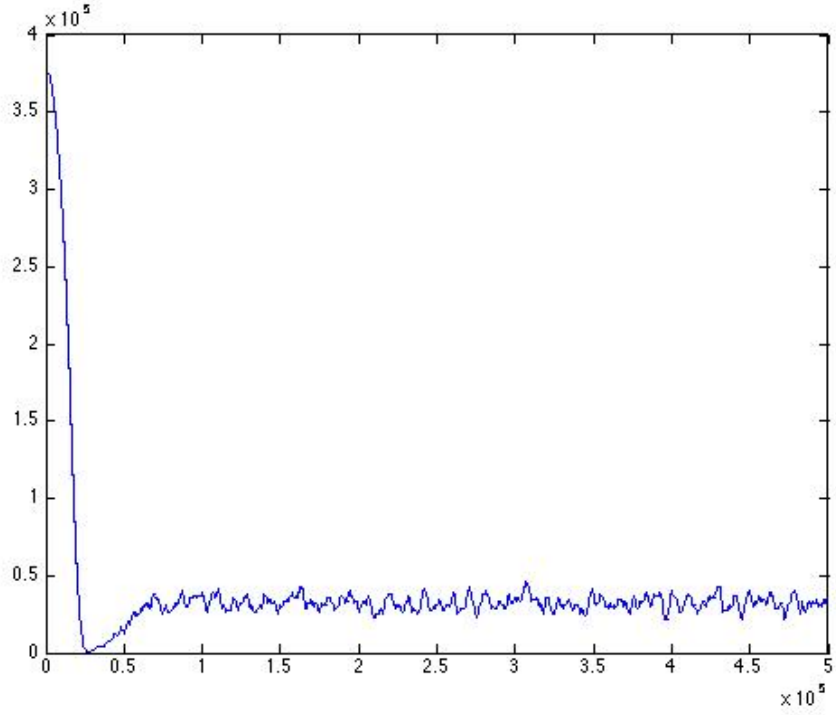


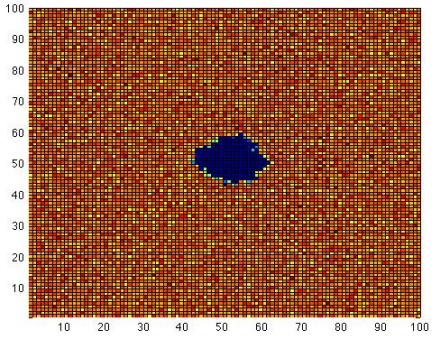
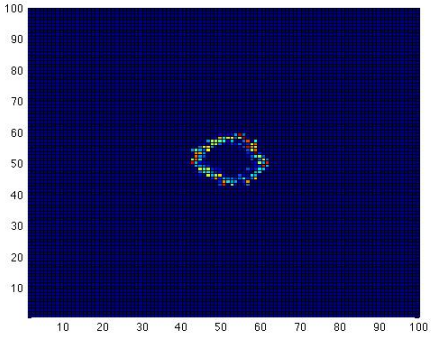
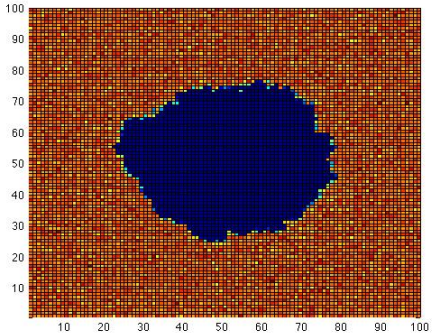
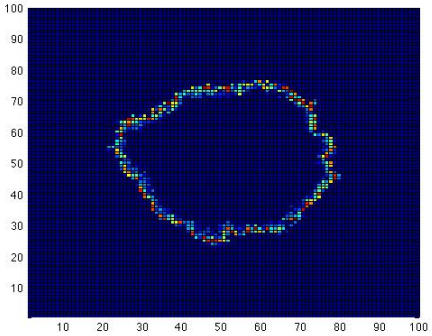
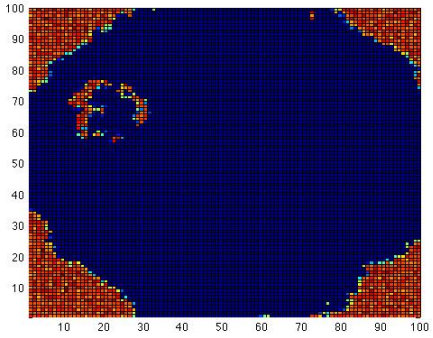
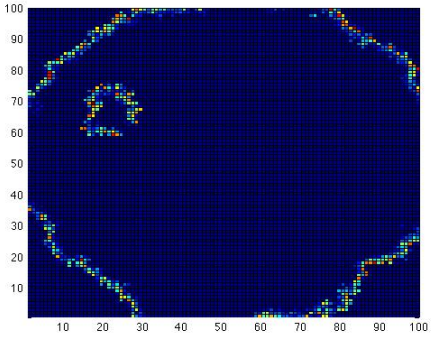
Table 6.2: Plots of the agent population in time. Populations are stable about long term average values. Hawk population time average is 15,820 (28.4%) while the number of Doves is 71.6% at 39,853. Standard deviations were 4,341 and 50,321 respectively.

Without Kairomone, Non-Averaged Payoff Structure

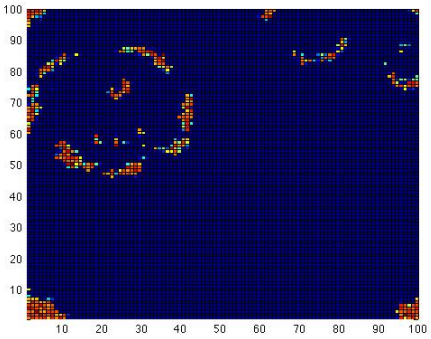
Here we consider the effect of removing from the payoff matrix the averaged payoff for a Hawk-Hawk contest. Instead in any given contest half of the Hawks will gain payoff V and the remainder will receive the cost $-C$. This change, which may have little effect for infinite, continuous, well mixed populations, has a significant effect on the finite population dynamics. In fact, in this case one might argue that this is not strictly a game, since the interaction cannot be formulated as a payoff matrix precisely because of the extra stochastic element that determines which Hawk gets what payoff. The results differ in character from the above case in which the payoff structure was the traditional averaged. The initial central Hawk gives rise to an expanding ring of Hawks that travel towards the edge of the grid. In the wake of this ring, behind the advancing wavefront of Hawks is left a void of totally depopulated grid space. A small number of Doves, three small colonies at the top of the grid, manage to survive the passing of this initial wavefront. They are accompanied by a small contingent of Hawks. These populations travel outward in waves to re populate the grid, forming a highly fragmented filamentary dynamic pattern. The Dove populations are followed very closely by the Hawks, and the spatial population profiles of both types are very similar in their details.

This simulation exhibited long term and sustained coexistence with fluctuations about seemingly stable long term averages. The duration of the simulation reported here is 500,000 time steps, or 50,000 generations, though from further simulations it is known that coexistence was maintained for in excess of 1.2 million time steps. Over the 500,000 time steps the mean number of Doves was 54,514 or some 75.3% of the population. Hawks then constituted a mean of 17,913 individuals, 24.7%. This is contrary to the well mixed 'classical' situation in which Hawk should be the Nash equilibrium and the only ESS. That the populations were relatively stable is shown

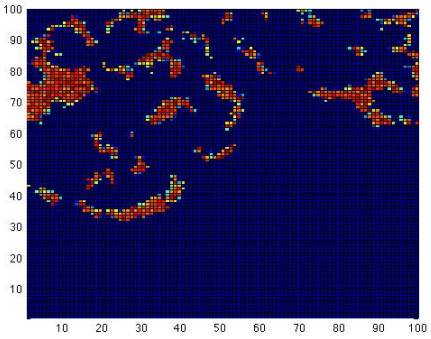
by the population plots below. The standard deviations in the numbers over the entire course of the simulation were 3,682 for the Hawks and 48,023 for the Doves.

Doves	Hawks
	
t = 3,500	t = 3,500
	
t = 10,000	t = 10,000
	
t = 20,000	t = 20,000

Hawks



t = 25,000



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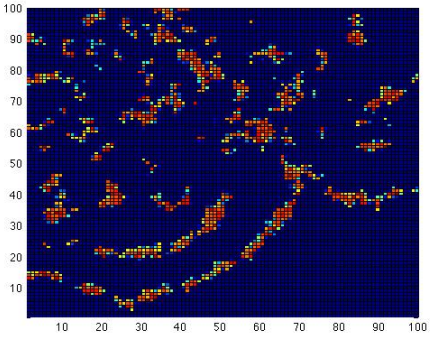
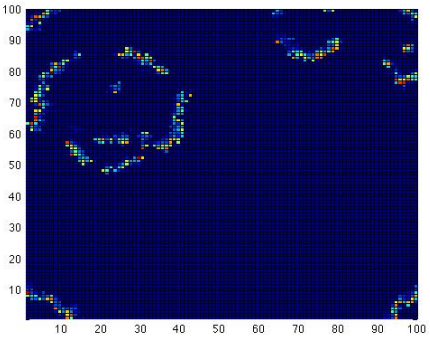
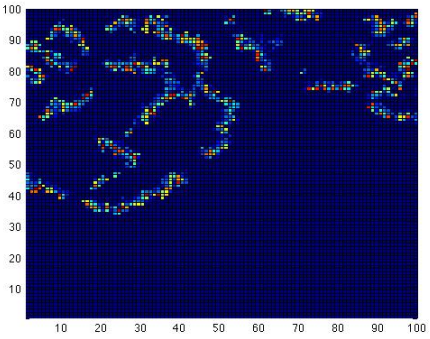


t = 40,000

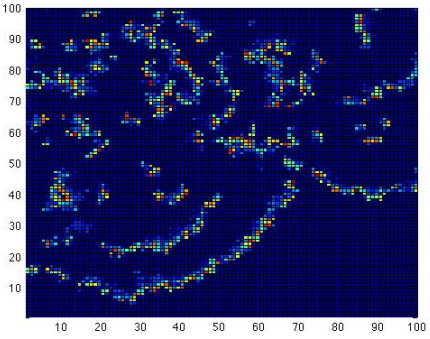
Doves



t = 25,000



t = 30,000



t = 40,000

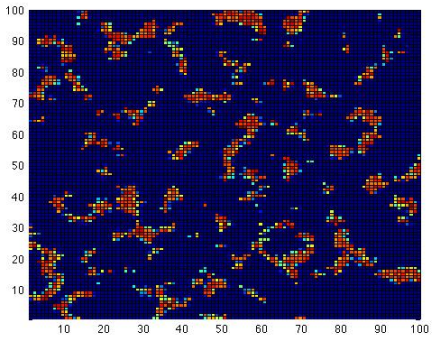
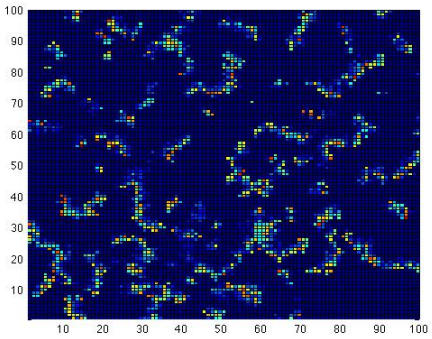
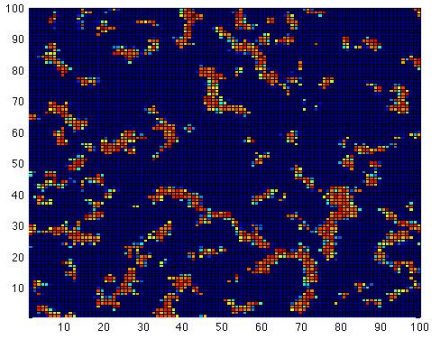
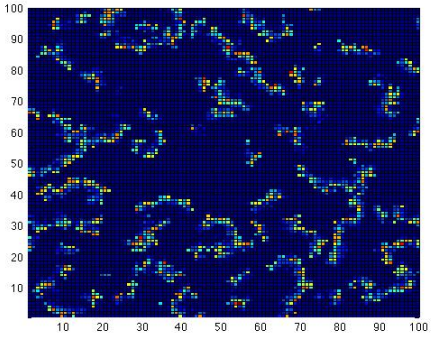
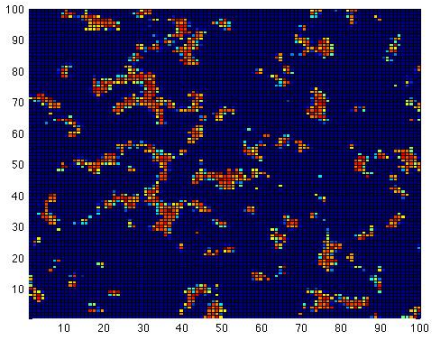
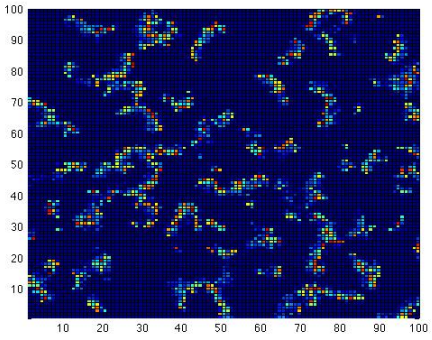
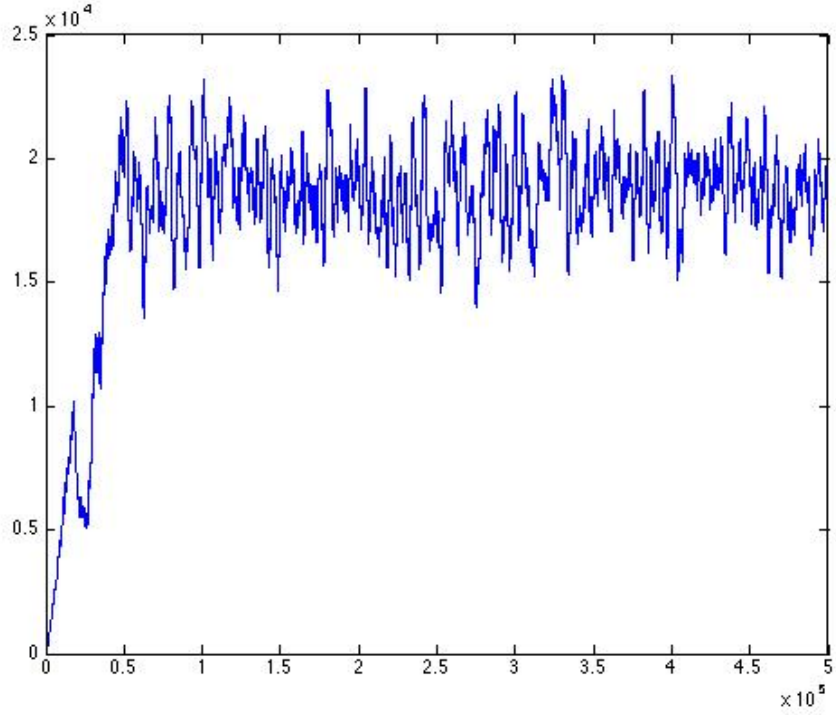
Doves	Hawks
	
t = 50,000	t = 50,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.3: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawk wavefront moves across the grid in a fragmented fashion. The remaining residual populations of Doves recover quickly and are highly clumped and fragmented. The Hawk population persists at a very low level.

Hawks



Doves

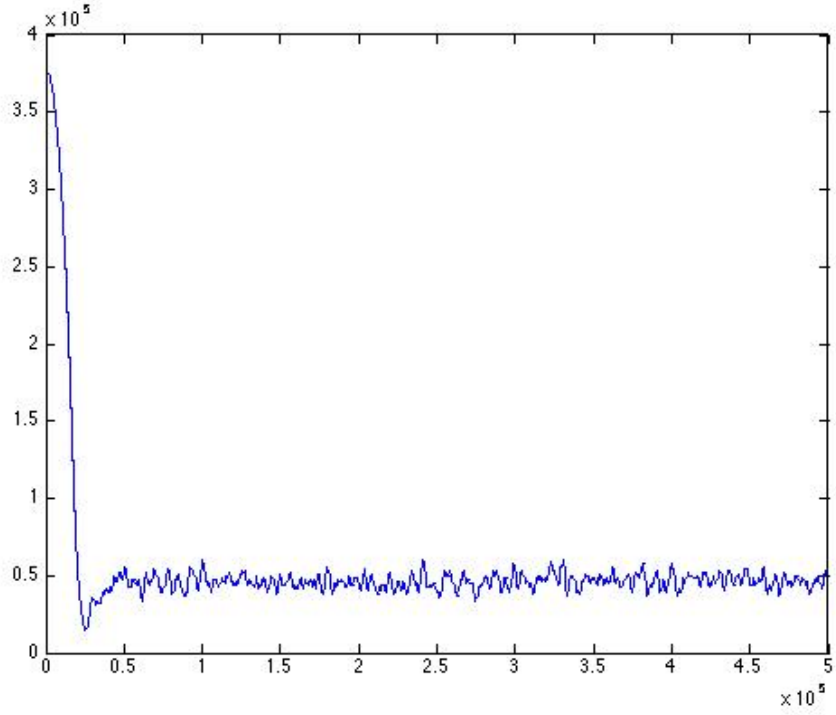
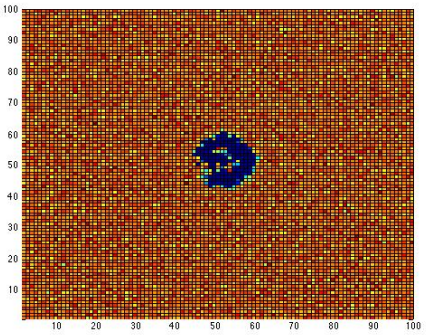


Table 6.4: Plots of the agent population in time. Populations are stable about long term average values. Hawk population time average is 17,913 (24.7%) while the number of Doves is 75.3% at 54,514. Standard deviations are 3,682 and 48,023 respectively.

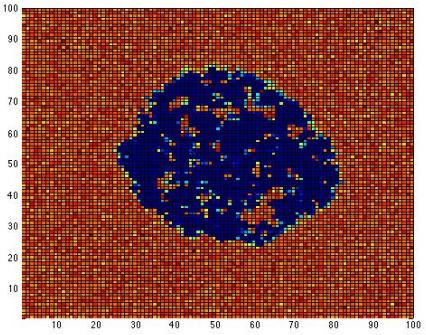
With Kairomone, Averaged Payoff Structure

Again a wavefront of invading hawks radiates outward from the grid centre, leaving in its wake a region of numerous scattered small colonies of Hawks and Doves that form a dynamically changing pattern. The mean population of Hawks over 500,000 time steps was 21,118, and the Dove population mean over the same period was 103,450. Thus Hawks comprised some 17% of the total population. Compared to the no kairomone case, there were more Hawks and less Doves. It is again to be of note that long term coexistence about stable long term averages was observed for this case, in which the Nash equilibrium and ESS of the underlying game should be to play Hawk.

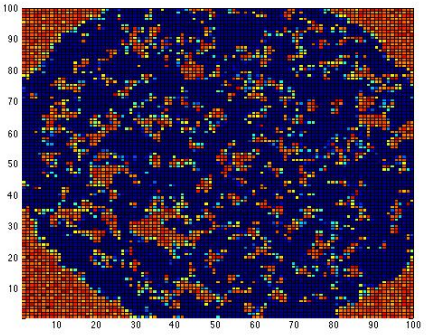
Doves



t = 3,500

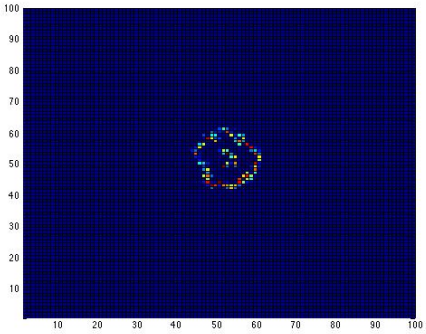


t = 10,000

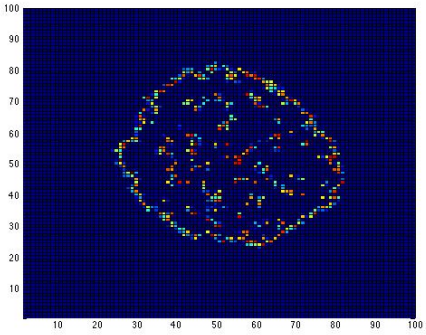


t = 20,000

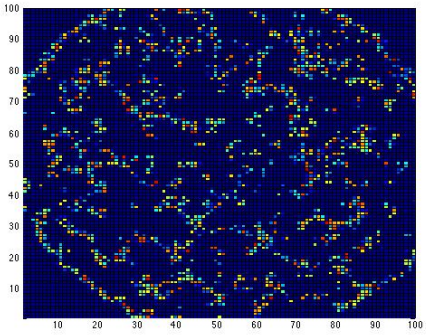
Hawks



t = 3,500



t = 10,000



t = 20,000

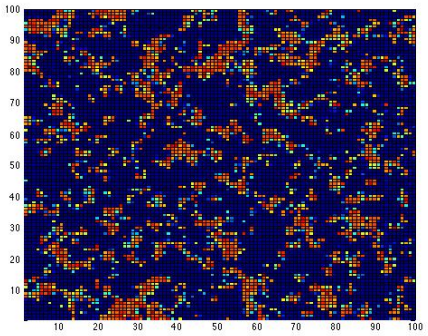
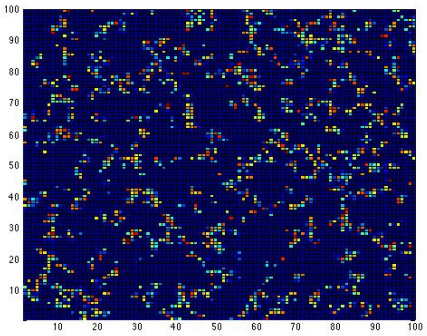
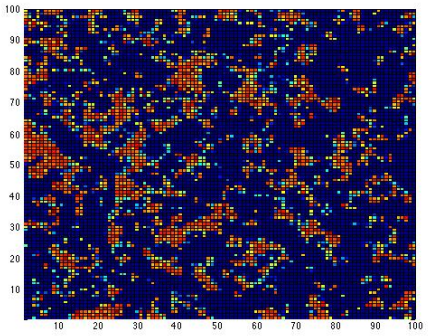
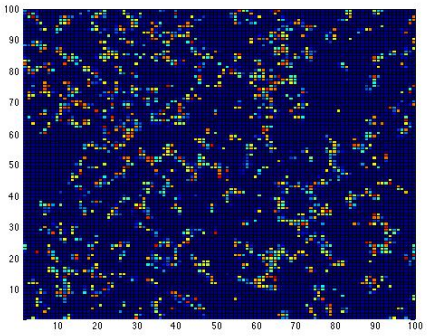
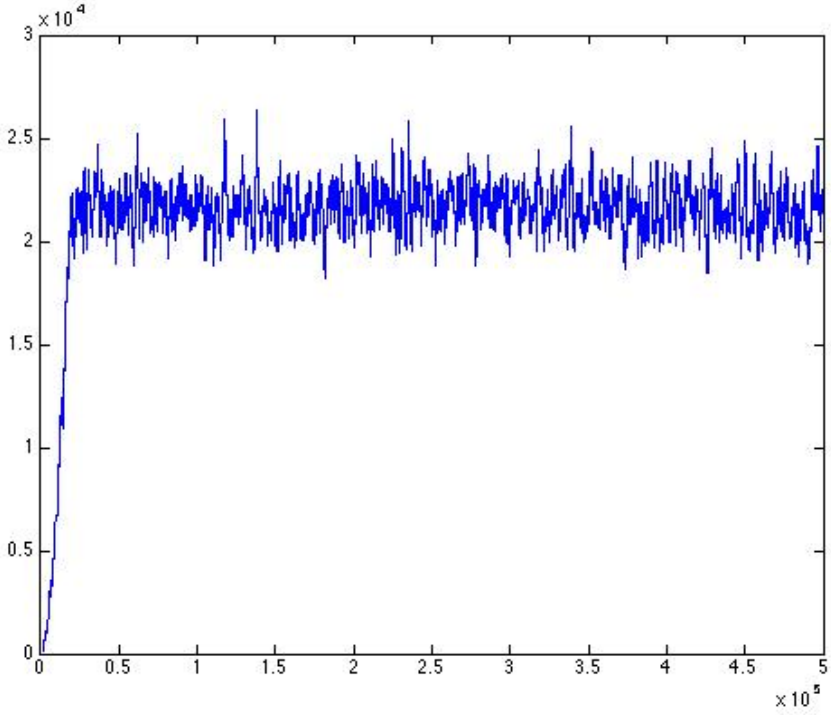
Hawks	Doves
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.5: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawk wavefront moves across the grid in a fragmented fashion. The remaining residual populations of Doves recover quickly and are highly clumped and fragmented. The Hawk population persists at a very low level.

Hawks



Doves

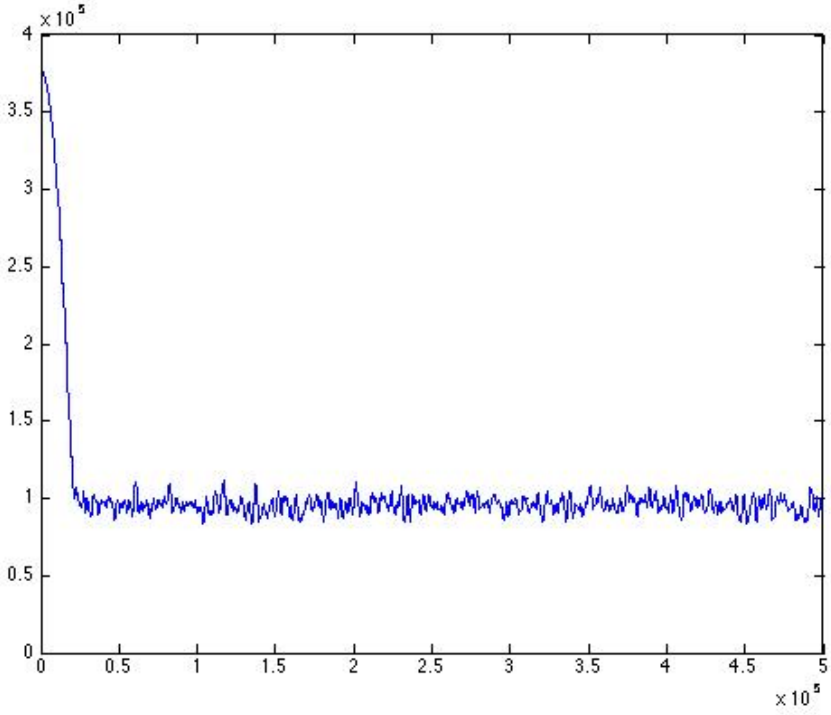
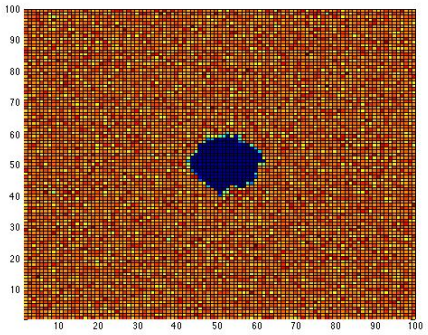


Table 6.6: Plots of the agent population in time. Populations are stable about long term average values. Hawk population time average is 21,118 (17%) while the number of Doves is 83% at 103,450. Standard deviations are 3,117 and 40,651 respectively.

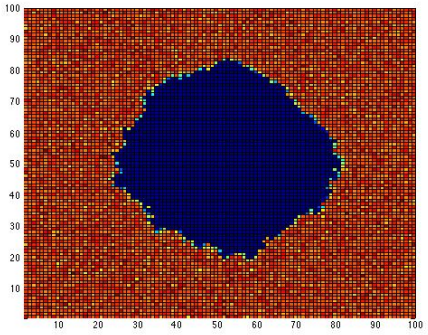
With Kairomone, Non-Averaged Payoff Structure for Hawks

Here we ran two simulations for the case of Kairomone secretion in the case in each Hawk-Hawk contest there was a definite winner, gaining payoff V, and a definite looser, payoff $-C$, the result of contest being decided by chance. As in the non-kairomone case, this makes a considerable difference to the dynamics. In the first simulation the Hawks became extinct, and in the second simulation both populations became extinct. The simulations begin in a fashion similar to that in the non kairomone case, with a near circular wavefront of advancing Hawks expanding into the established Dove population, leaving mostly empt unpopulated grid space as it passed. In the first run two small residual mixed populations survived for a short period at the bottom portion of the grid. These became extinct by t = 41,600. A small isolated population of Doves in the top right hand corner grew to repopulate the entire grid to its carrying capacity of approximately 360,000 individuals. In the second run the expanding wavefront of Hawks leaves no residual populations to survive and mutual extinction occurs by t = 26,000. In this case, the Hawks, being parasitic upon the Doves, could not survive without Doves. After the Doves became extinct, the Hawks very quickly followed, as they were not able to gather sufficient payoff from their Hawk-Hawk interactions to sustain a viable population.

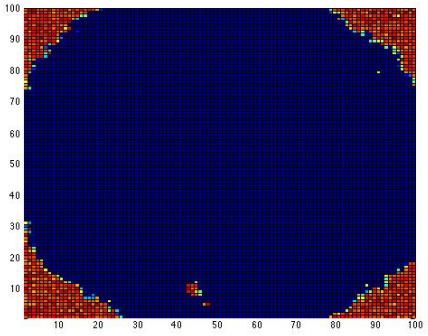
Doves



t = 3,500

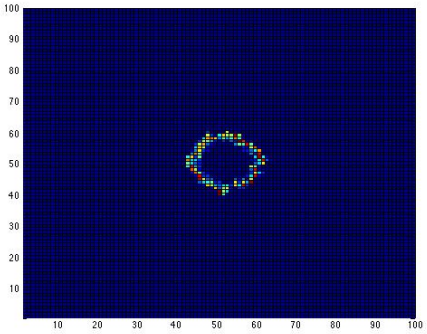


t = 10,000

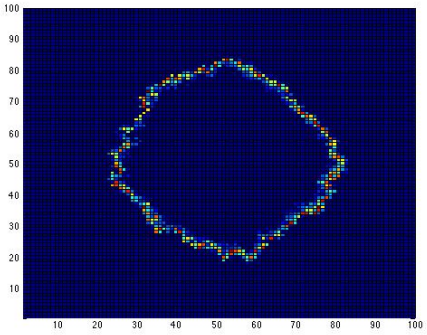


t = 20,000

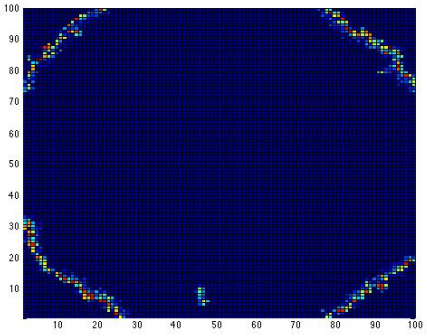
Hawks



t = 3,500



t = 10,000



t = 20,000

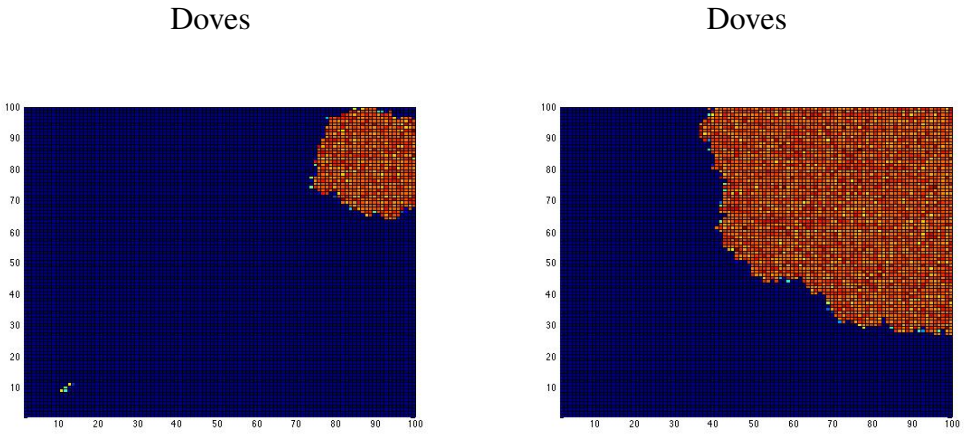
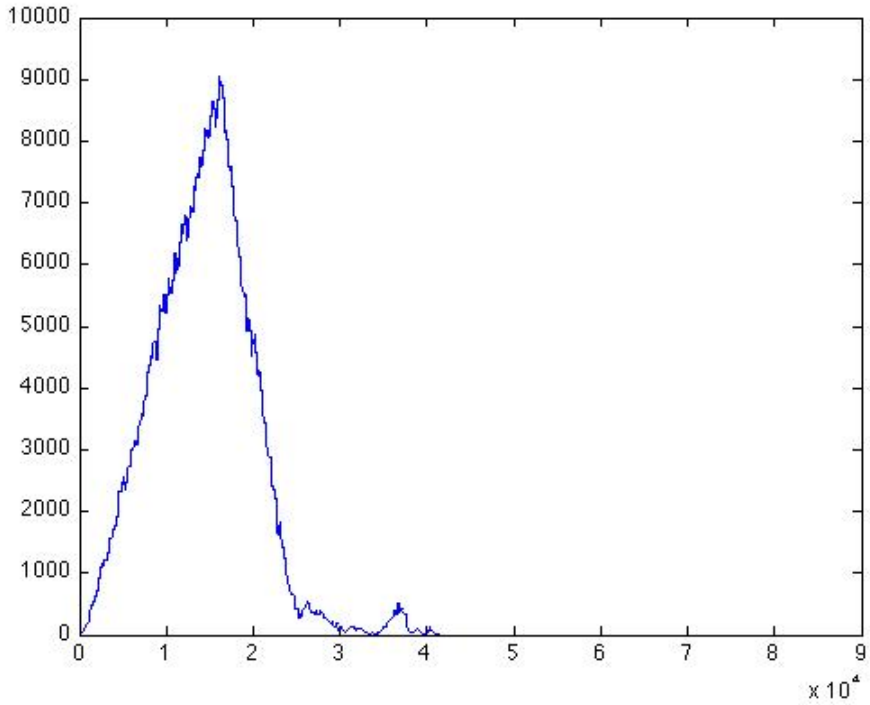


Table 6.7: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawk wavefront moves across the grid. The Hawks become extinct as this wavefront encounters the edge of the grid. A remaining residual population of Doves recovers quickly and expands to colonise the entire grid to the carrying capacity.

Hawks



Doves

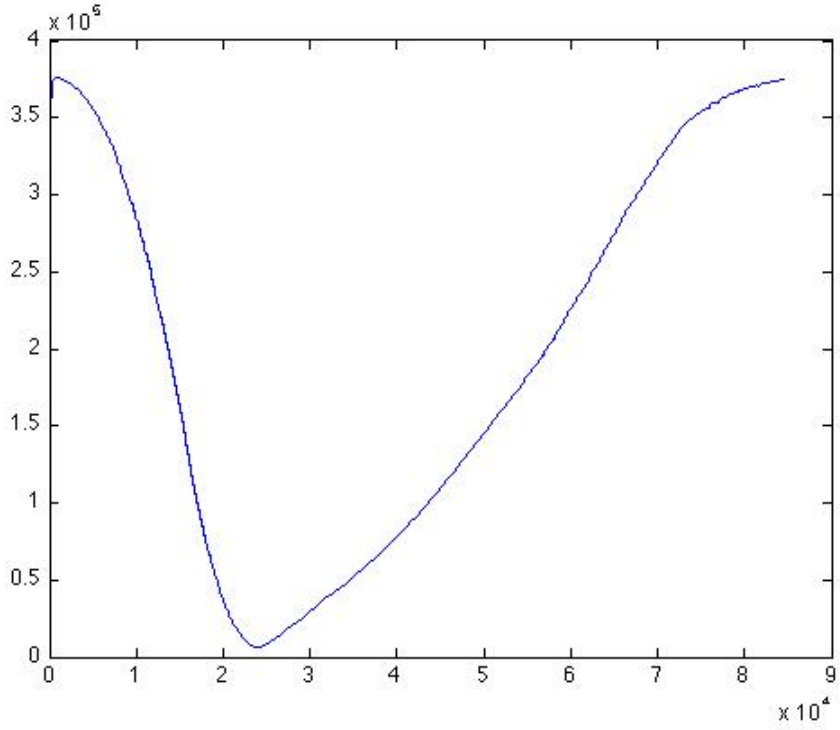


Table 6.8: Plots of the agent population in time. The Hawks become extinct as the invading wavefront reaches the edge of the grid, whilst a single colony of Doves recovers to re-seed the entire grid to capacity

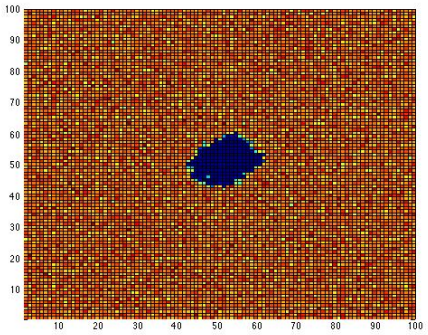
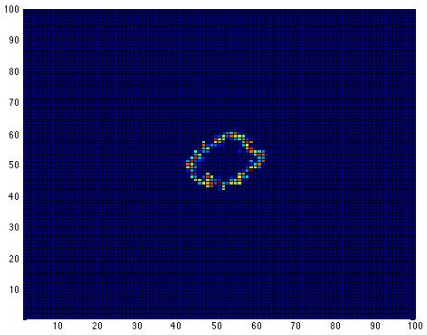
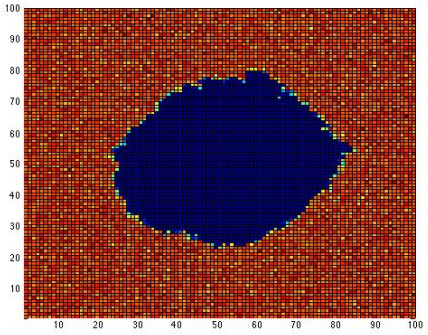
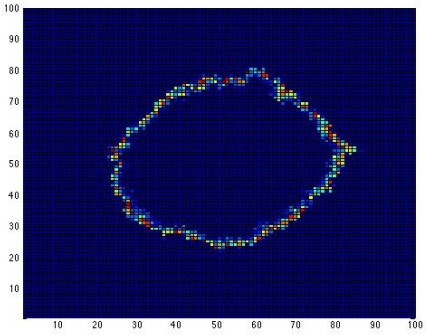
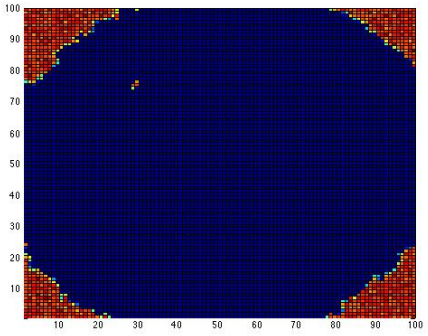
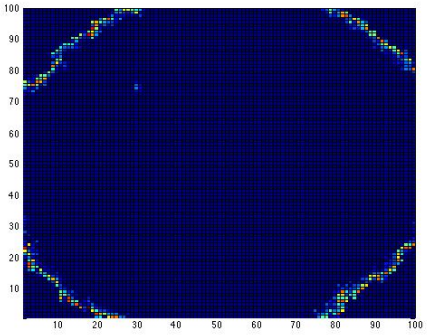
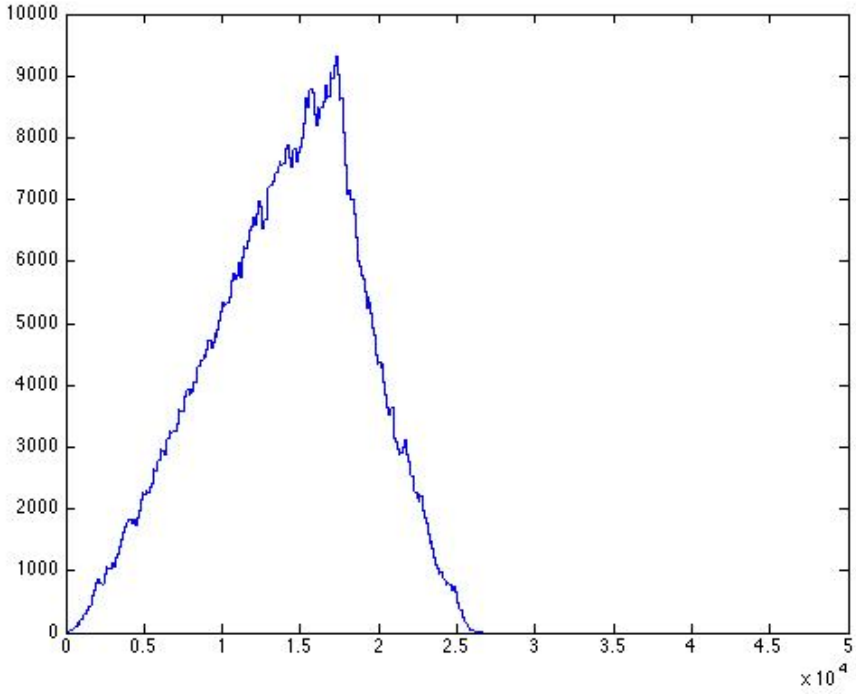
Doves	Hawks
	
t = 3,500	t = 3,500
	
t = 10,000	t = 10,000
	
t = 20,000	t = 20,000

Table 6.9: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion ($\nu = 1$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawk wavefront moves across the grid. The Hawks become extinct as this wavefront encounters the edge of the grid. A remaining residual population of Doves recovers quickly and expands to colonise the entire grid to the carrying capacity.

Hawks



Doves

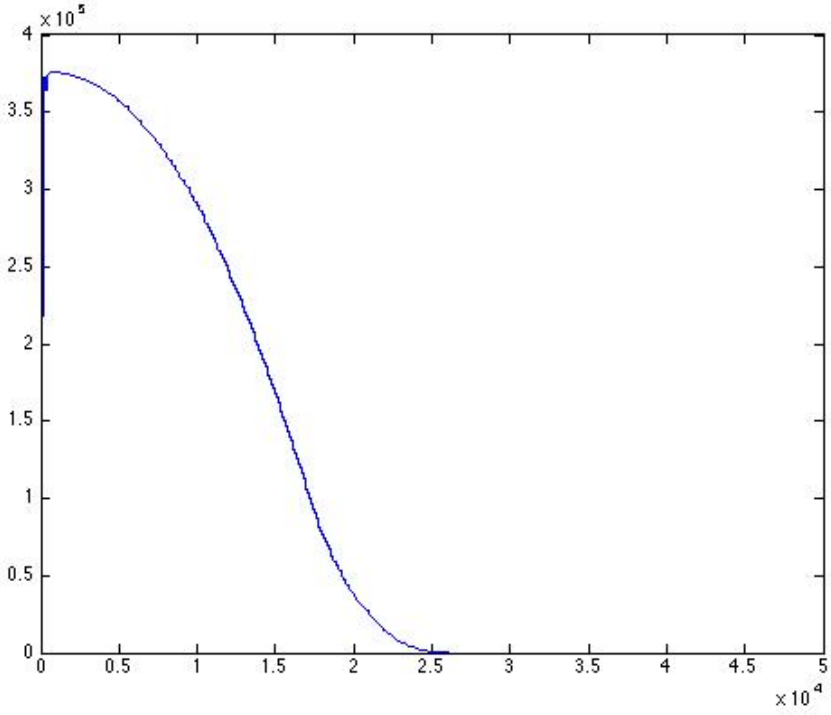


Table 6.10: Plots of the agent population in time. The Hawks become extinct as the invading wavefront reaches the edge of the grid, whilst a single colony of Doves recovers to re-seed the entire grid to capacity

Discussion

Of the four scenarios considered in this section, three resulted in long term stable mutual coexistence of Hawks and Doves, whilst in the final case either one or both populations became extinct. These results are contrary to those expected in an infinite, well mixed population. In that case, the ESS is to play Hawk. As Dove is not an ESS, a population of Doves should be susceptible to invasion by Hawks. Thus these simulations highlight two aspects that might well be considered when applying game theory to finite populations. One is that spatial distribution of agents can be of significant impact to survival, another is that the absolute and relative magnitudes of the payoffs awarded in an interaction are significant. In this case, the Hawk-Hawk payoff was insufficient to allow an isolated population of Hawks to be reproductively viable. By this mechanism, the Hawks were dependent for their continuation upon the presence of a population of Doves. In this sense the Hawks were parasitic upon the Doves.

In the case of the averaged Hawk payoff structure, where in a Hawk-Hawk contest, each receives payoff $\frac{1}{2}(V-C)$, allowing the secretion of kairomone was beneficial to the Hawks, with the population rising in both absolute terms (from 13,816 to 21,118) and percentage terms (from 10% to 17%). Conversely, the Dove population fell from 128,680 (90%) to 103,450 (83%). The obvious explanation is that kairomone secretion had allowed the parasitic Hawks to more efficiently locate the Doves. The effect of kairomone secretion upon the non-averaged payoff structure simulations was to destabilise mutual coexistence by allowing the Hawks to become too efficient at locating the Doves.

In the case of no kairomone secretion, comparing the simulations using the averaged and the non-averaged payoff structure, it seems that the non-averaged structure was on the hole beneficial to the survival of the Hawks. Hawk populations were then 17,912

(24.8%) compared to 13,816 (10%) in the averaged case. Correspondingly, Dove populations adjusted from 128,680 (90%) to 54,352 (75.2%). This represents a dramatic decrease in the Dove population to some 42% of its averaged payoff structure value. This kind of dramatic difference in both absolute and percentage population values between the two payoff structures illustrates another means by which the results of a finite population individual based model may differ from those expected from an infinite well-mixed population.

There was a notable change in the character of the spatial distribution in changing from an averaged payoff structure to a non averaged structure. In the averaged case the distribution seems to be of the form of elongated, filamentary concentrations of agents that are constantly moving in a manner reminiscent of wavefronts. In the one non-averaged case in which the coexistence was stable, the spatial distribution was notable more fragmented, with many smaller disconnected population centres of agents of both types. This difference is not betrayed by the gross simulation results of average populations as summarised in the below table.

Table 6.11: Comparison of Simulation Results for Case $V = 0.04$, $C = 0.03$

Case	Payoff Structure	Kairomone (ν)	Hawk Mean	Dove Mean	Comment
1	Averaged	0	15,820 (28.4%)	39,853 (71.6%)	Coexistence
2	Not averaged	0	17,912 (24.8%)	54,352 (75.2%)	Coexistence
3	Averaged	1	21,118 (17%)	103,450 (83%)	Coexistence
4a	Not averaged	1	0	0	Extinction
4b	Not averaged	1	0	360,000	Doves survive

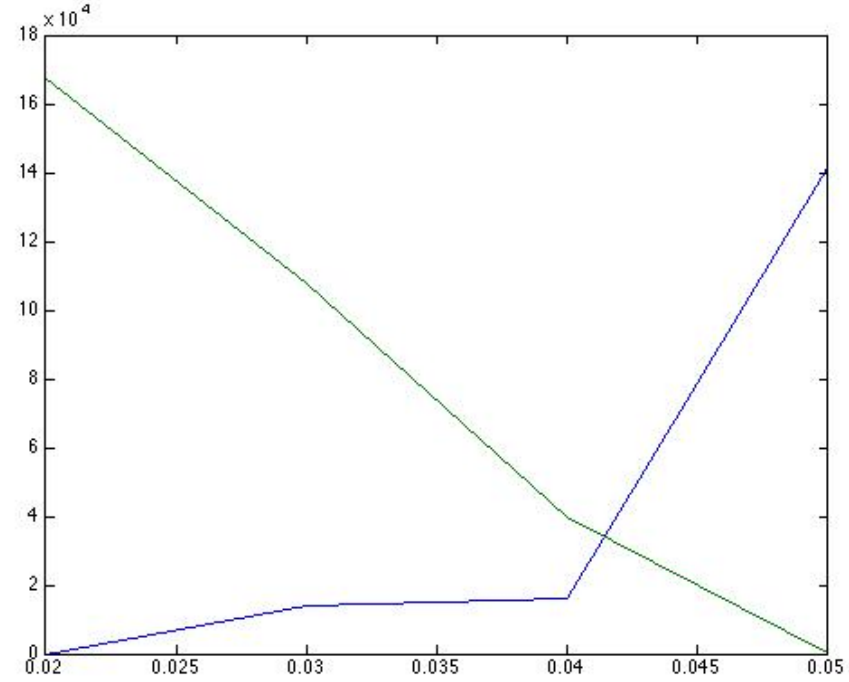
The Effect of Varying V

In this section we keep the cost of injury C constant at $C = 0.03$ and investigate the effect of varying the reward V on the population dynamics for each of the four simulation regimes.

Averaged Payoff Structure Without Kairomone

It was found that there was a relatively narrow range of values of V over which long term coexistence could be observed. For small values of V, for which the cost of injury exceeded the reward payoff, the Hawks generally became extinct, as one might expect. For larger values of V the Hawks remained in a stable coexistence with the Doves. For $V > 0.05$ it was the Doves that became extinct and the Hawks took over the entire population. So actually for most of the parameter ranges the prevailing situation was a monomorphic population of either Hawks or Doves, with coexistence of both obtaining in a limited parameter range occupying the boundary between the ranges for the monomorphic cases.

Population as a Function of V



Percentage Population Composition as a Function of V

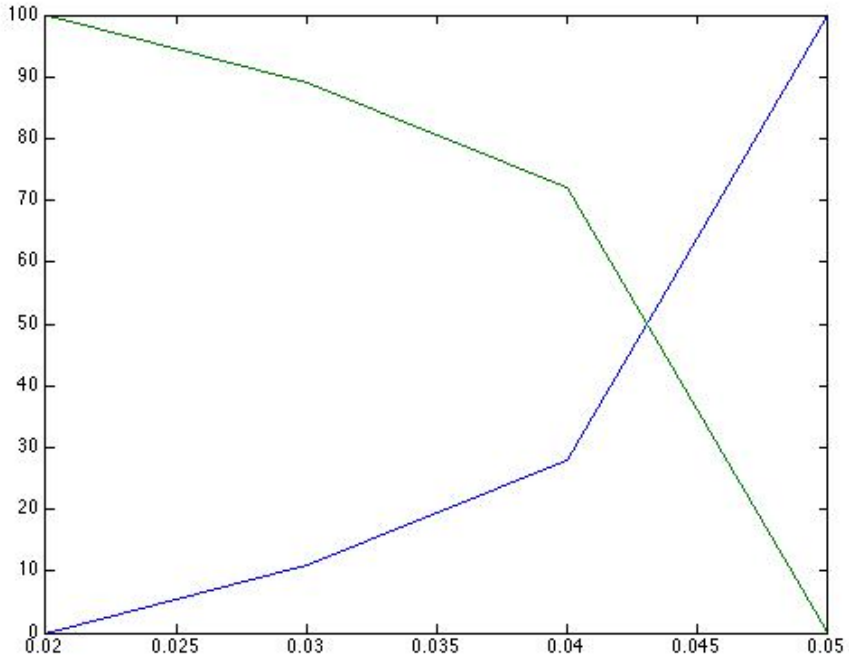
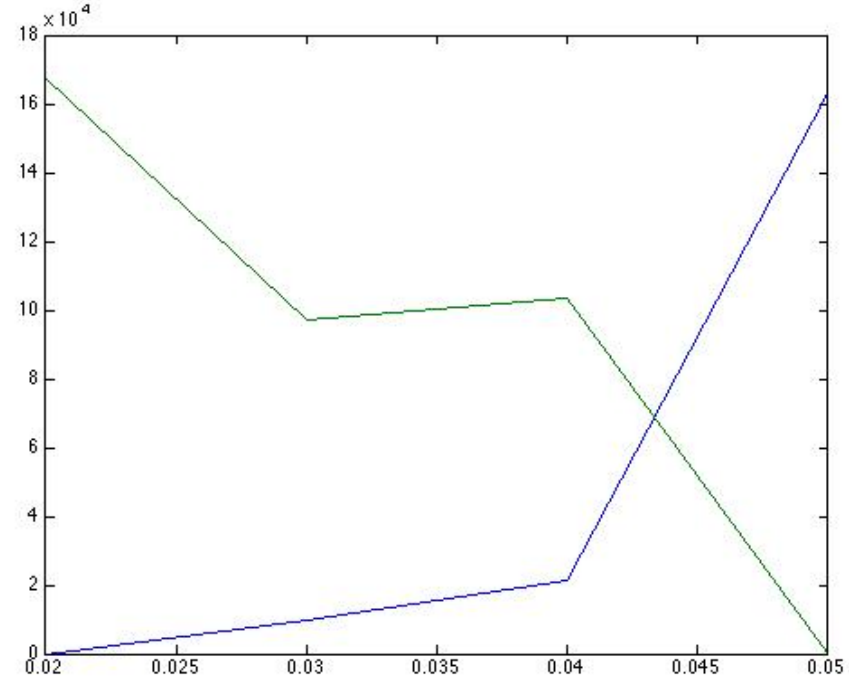


Table 6.12: The case of no kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

Non-Averaged Payoff Structure Without Kairomone

Varying V in the presence of a kairomone for the individual payoff structure we find broadly similar behaviour to the previous case above. Coexistence was observed for the parameter range $0.02 < V < 0.05$, with the population being monomorphic in Hawks above this range and in Doves below this range.

Population as a Function of V



Percentage Population Composition as a Function of V

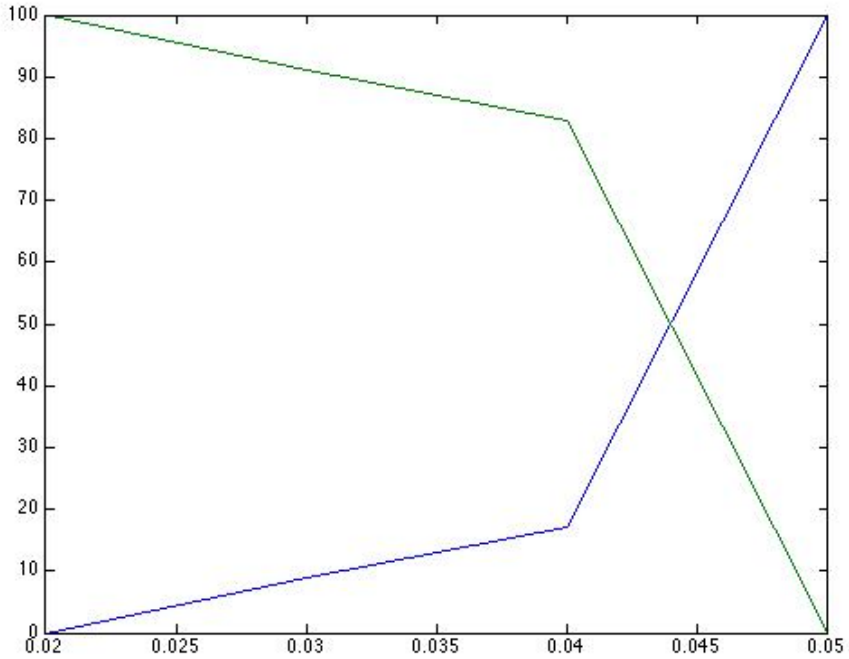
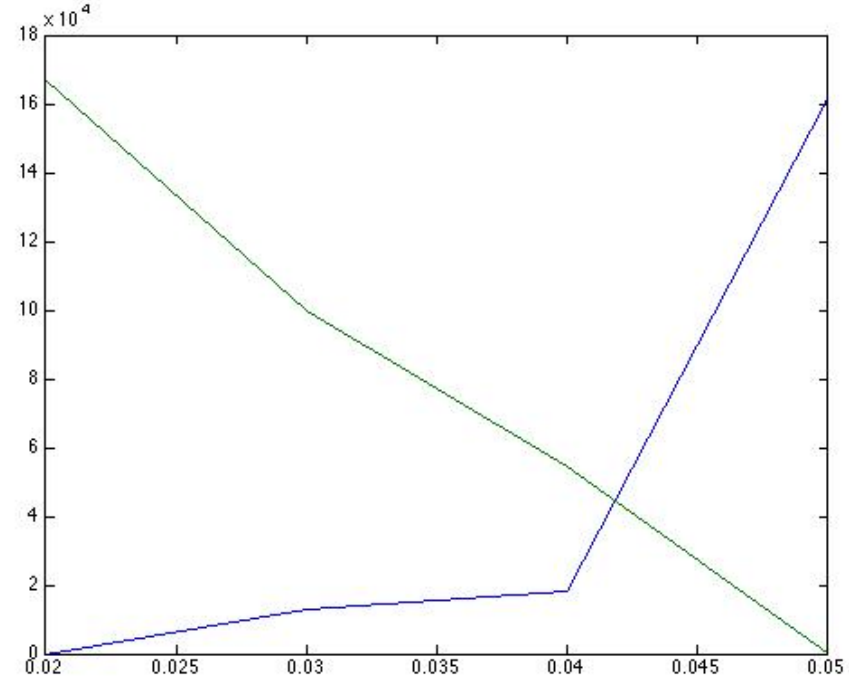


Table 6.13: The case of no kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

Averaged Payoff Structure Without Kairomone

Varying V in the presence of a kairomone for the individual payoff structure we find broadly similar behaviour to the previous case above. Coexistence was observed for the parameter range $0.02 < V < 0.05$, with the population being monomorphic in Hawks above this range and in Doves below this range.

Population as a Function of V



Percentage Population Composition as a Function of V

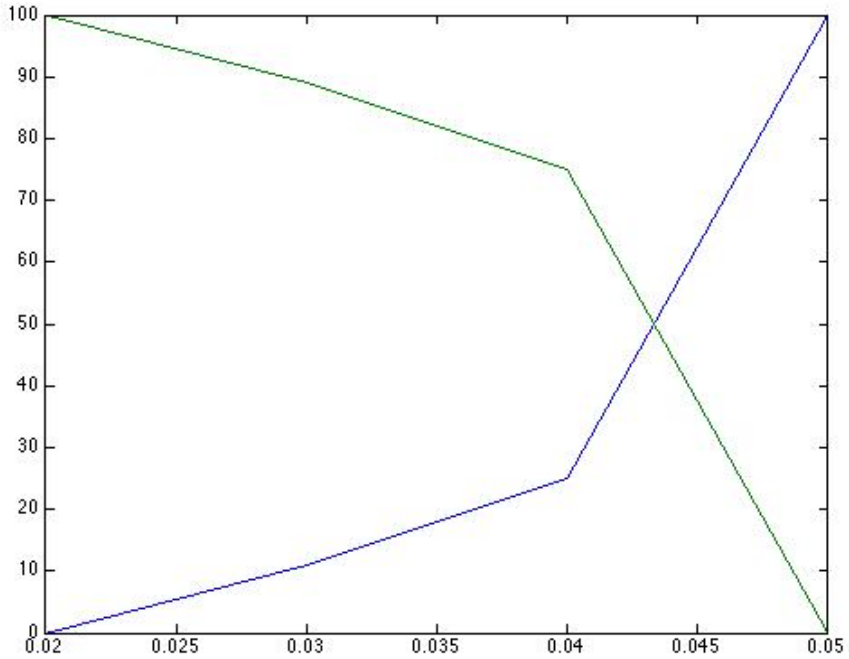
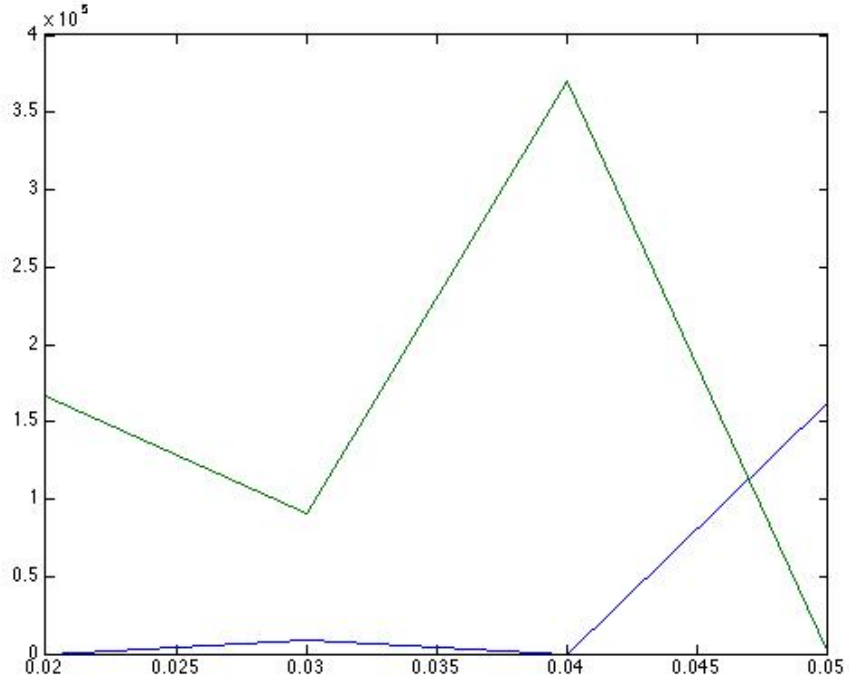


Table 6.14: The case of no kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

Non-Averaged Payoff Structure With Kairomone

Varying V in the presence of a kairomone for the individual payoff structure we find broadly similar behaviour to the previous case above. Coexistence was observed for the parameter range $0.02 < V < 0.05$, with the population being monomorphic in Hawks above this range and in Doves below this range. However, in this overlap region the population of Hawks is generally much lower than for the cases considered above. The change over from majority Dove to majority Hawk population was altogether much more rapid. Hawks actually became extinct in one of the simulations in this intermediate parameter range, illustrating how the low level of the Hawk population was particularly susceptible to chance extinction due to an unfavourable spatial configuration.

Population as a Function of V



Percentage Population Composition as a Function of V

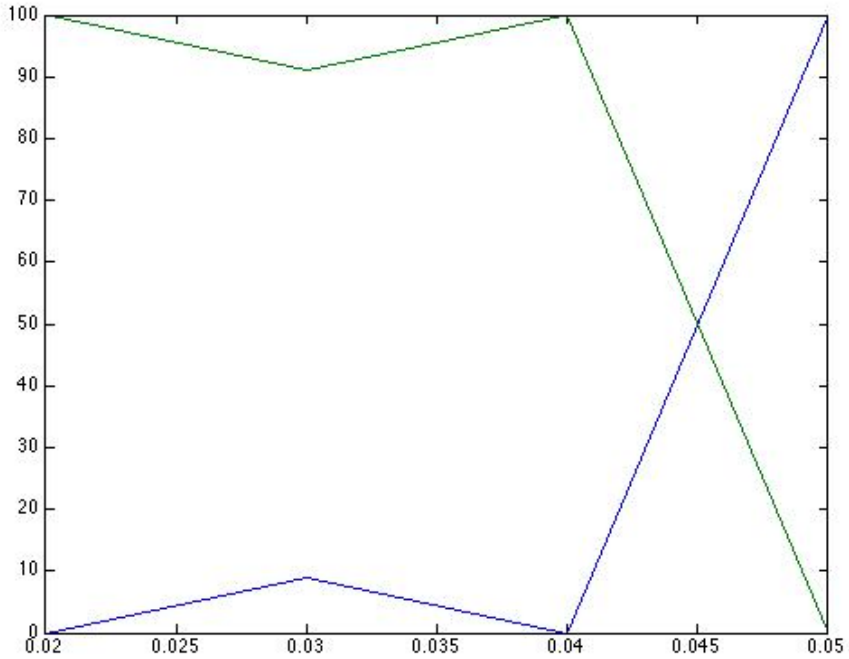


Table 6.15: The case with kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

Summary

Four simulation types were considered, being with and without kairomone and an averaged or an individual payoff structure. For all four regimes, the game theory parameter V, being the reward value, was varied and all four regimes exhibited broadly the same range of V over which sustained coexistence was observed. This range for V was $0.02 < V < 0.05$. For values of V above this range the long term population consisted entirely of Hawks, and for the region below this range the long term population was entirely composed of Doves. So mutual coexistence was observed in a parameter range that separated the domains two of monomorphic stability.

6.2 Non-Synchronous Generations

When considering the synchronous generation model, we set $V = 0.04$ and $C = 0.03$ and found that there was mutual coexistence of both strategies in most cases. However, in moving to non-synchronous generation, this coexistence is completely destabilised, and all simulations end in mutual extinction, regardless of the Hawk-Hawk payoff structure or the secretion of kairomone. The Hawks act like an extremely virulent infection that annihilates its host and thereby itself as well. We therefore need a new set of parameters to act as a base from which we may explore the parameter space. To find stable coexistence of Hawks and Doves we will need to reduce the virulence of the Hawks, which means that we should consider a reduced value of V. We will find that mutual coexistence may be re-established for $V = 0.03$ and $C = 0.04$. In the classical evolutionary game theory analysis, the ESS would be for an agent to play Hawk with probability $3/4$. Furthermore it can be shown that for a population polymorphic in the purse strategies that is infinite and well mixed, that the proportion of Hawks should be $3/4$ and Doves should be $1/4$. Naively one might expect broadly similar behaviour in

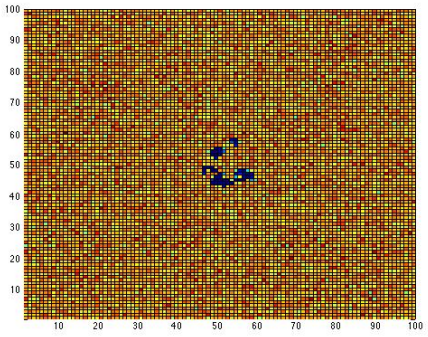
a spatial population, however the results presented below differ from such expectations in both the proportion of Hawk and Dove players and in the range of parameter values in which coexistence can be observed.

Averaged Payoff Structure Without Kairomone Secretion

The advancing wavefront nature of invading Hawks that was evident in previous simulation was not present in this case. Rather the Hawks gradually percolated into the population in an uneven advance. The Doves appear to be evenly distributed over much of the grid, punctuated by numerous small regions in which the Hawks are active. The Hawk population persists at a relatively low level with an average over five hundred thousand timesteps of 7,039 individuals, representing 3.5% of the population. The Dove population at 195,500 individuals, shows only highly localised depletion due to the presence of the Hawks. The carrying capacity of the grid for this parameter range is approximately 270,000 Doves, thus the presence of a small number of Hawks has the effect or reducing the Dove population by some 27.5%. Which is to say that the 7,039 Hawks have acted to reduce the grid Dove population by on average 74,500 individuals. The Hawks thereby resemble an endemic parasitism or disease.

Doves

Hawks



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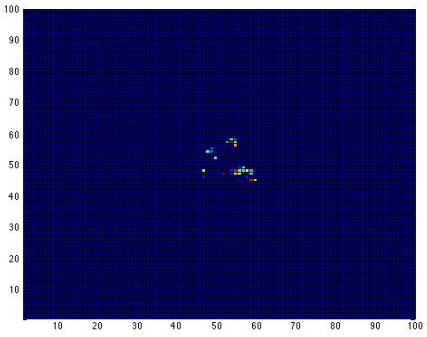
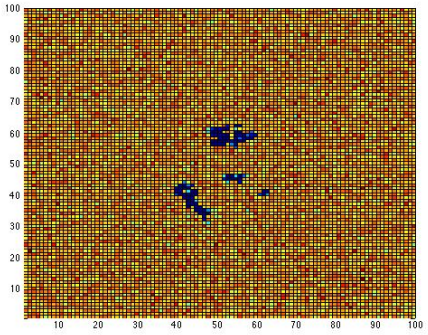


t = 3,500



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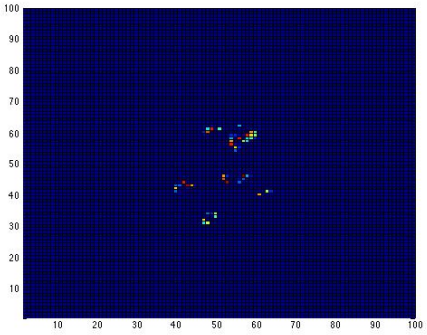

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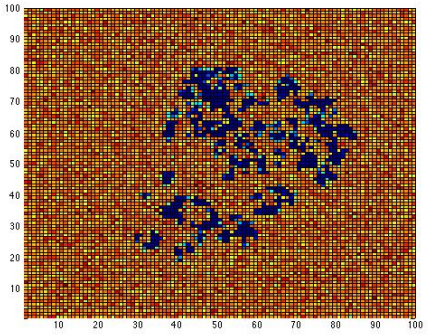
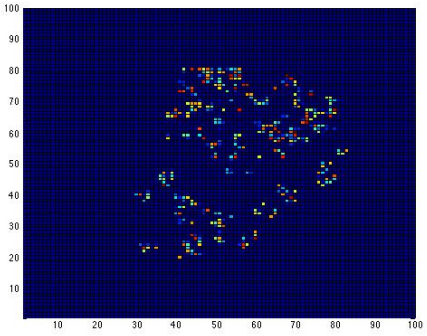
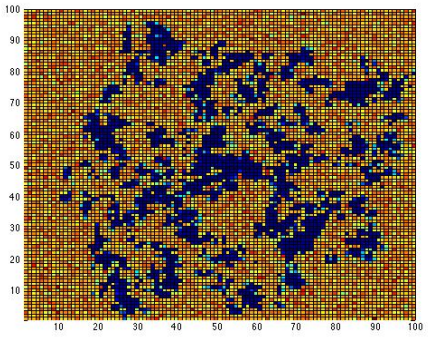


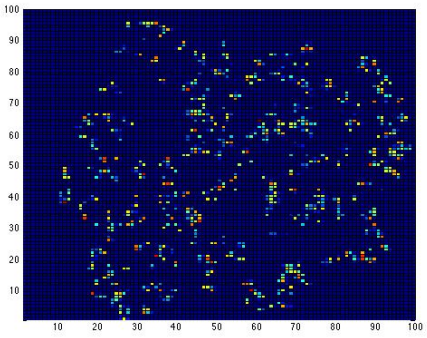
t = 20,000



t = 20,000



t = 30,000



t = 30,000

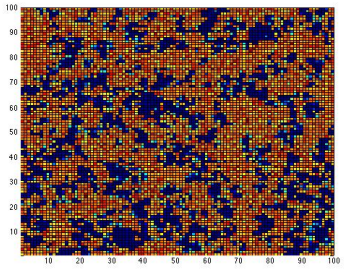
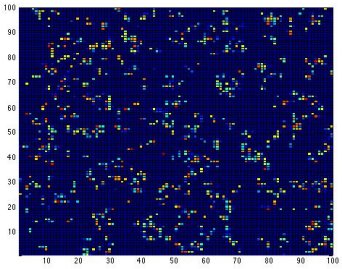
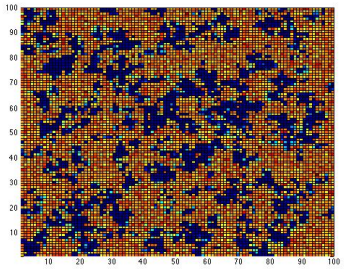
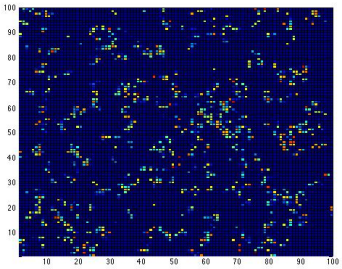
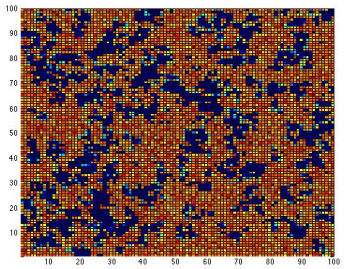
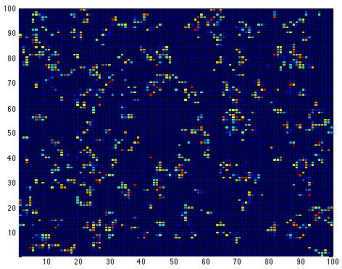
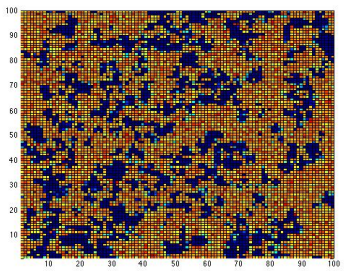
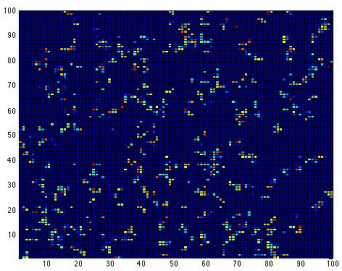
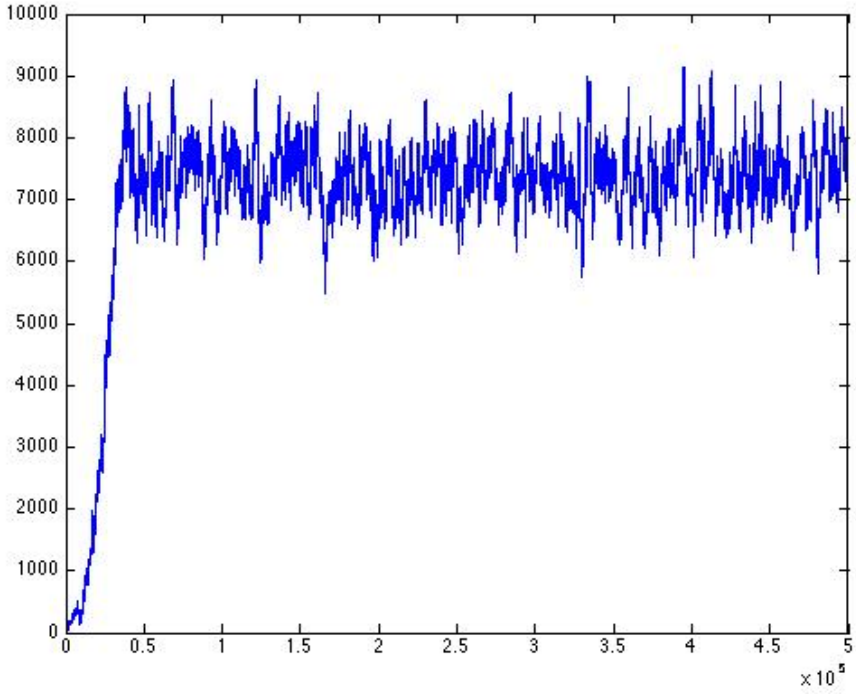
Doves	Hawks
	
t = 40,000	t = 40,000
	
t = 50,000	t = 50,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.16: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawks diffuse into the grid. Hawks persist at low levels on a substantial background Dove population.

Hawks



Doves

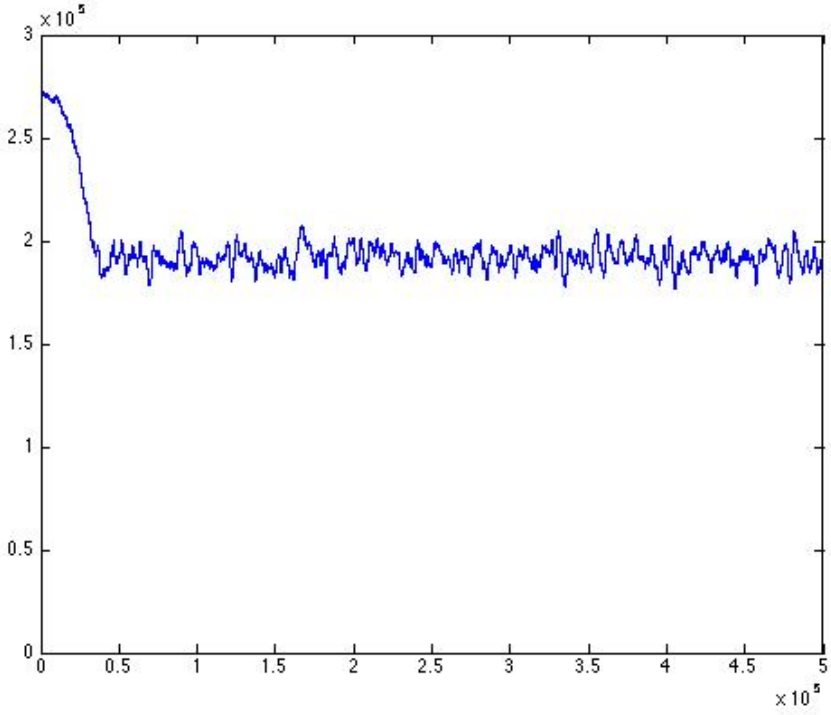


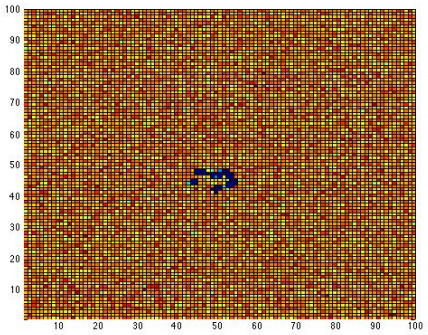
Table 6.17: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a low level of 7,039 individuals, 3.5% of the population. The Hawk population standard deviation was 1,489, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 195,590 individuals with a standard deviation of 16,288.

Averaged Payoff Structure With Kairomone Secretion

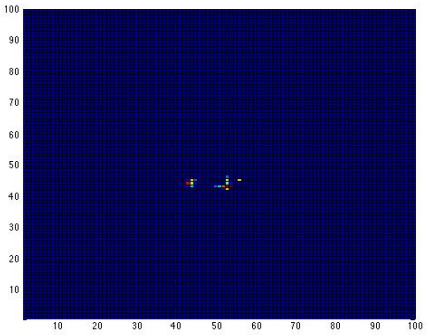
The advancing wavefront nature of invading Hawks that was evident in previous simulation was not present in this case. Rather the Hawks gradually percolated into the population in an uneven advance. The Doves appear to be evenly distributed over much of the grid, punctuated by numerous small regions in which the Hawks are active. The Hawk population persists at a relatively low level with an average over five hundred thousand timesteps of 4,631 individuals, representing 2.3% of the population. The Dove population at 197,080 individuals, again shows only highly localised depletion due to the presence of the Hawks. This represents some 73% of the grids Dove carrying capacity. Thus a contingent of 4,631 Hawks has reduced the Dove population by approximately 73,000 individuals.

Doves

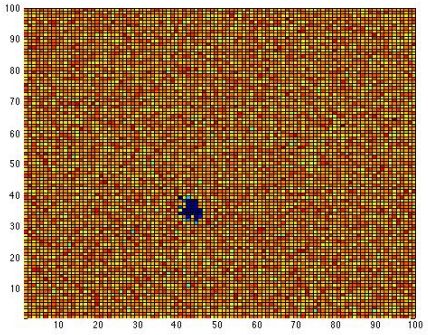
Hawks



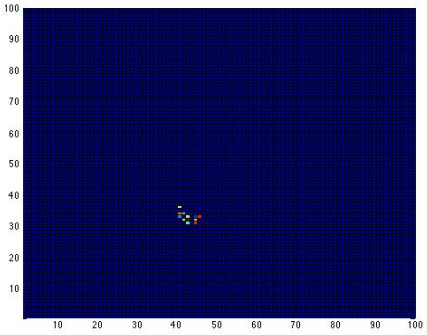
t = 3,500



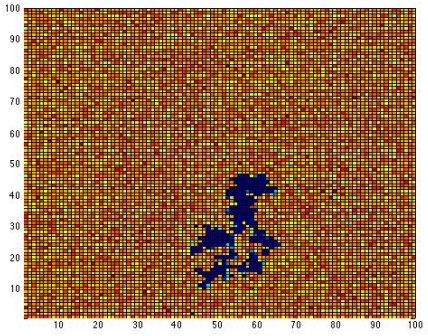
t = 3,500



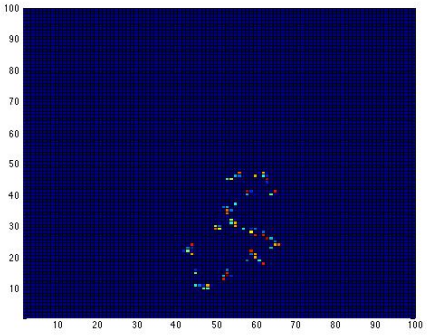
t = 10,000



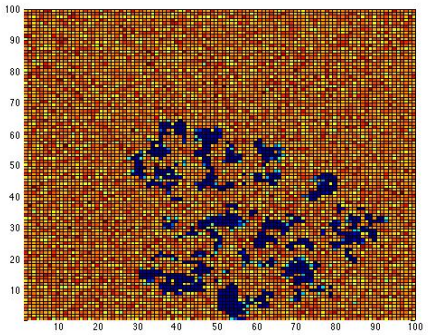
t = 10,000



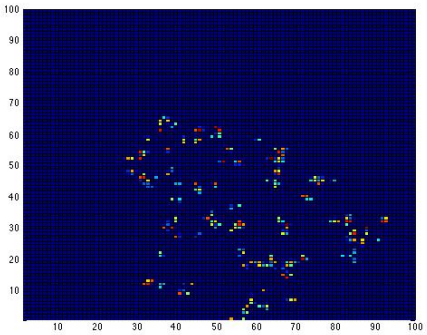
t = 20,000



t = 20,000



t = 30,000



t = 30,000

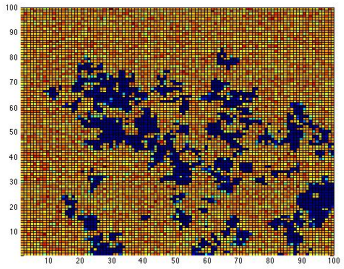
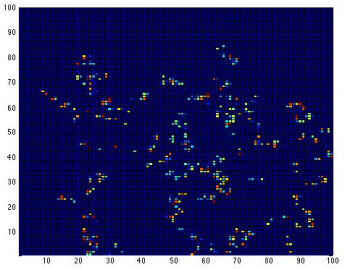
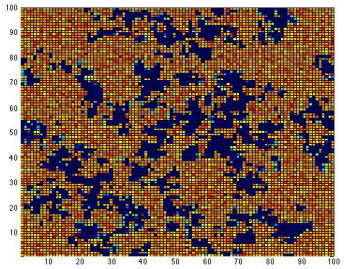
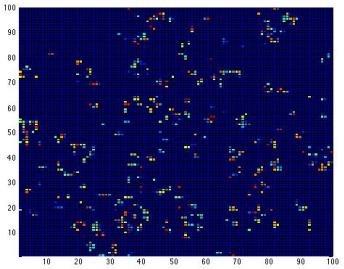
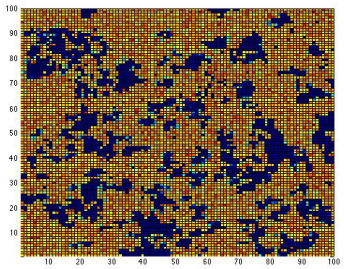
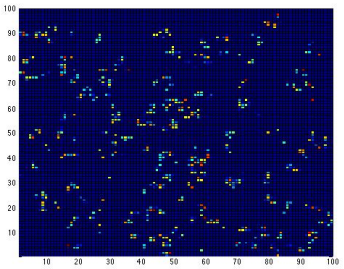
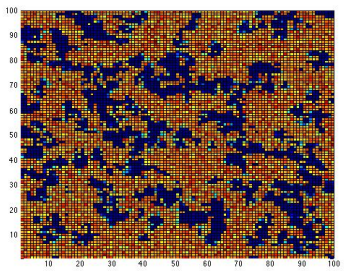
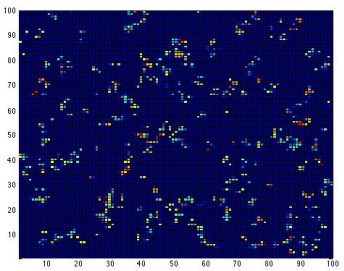
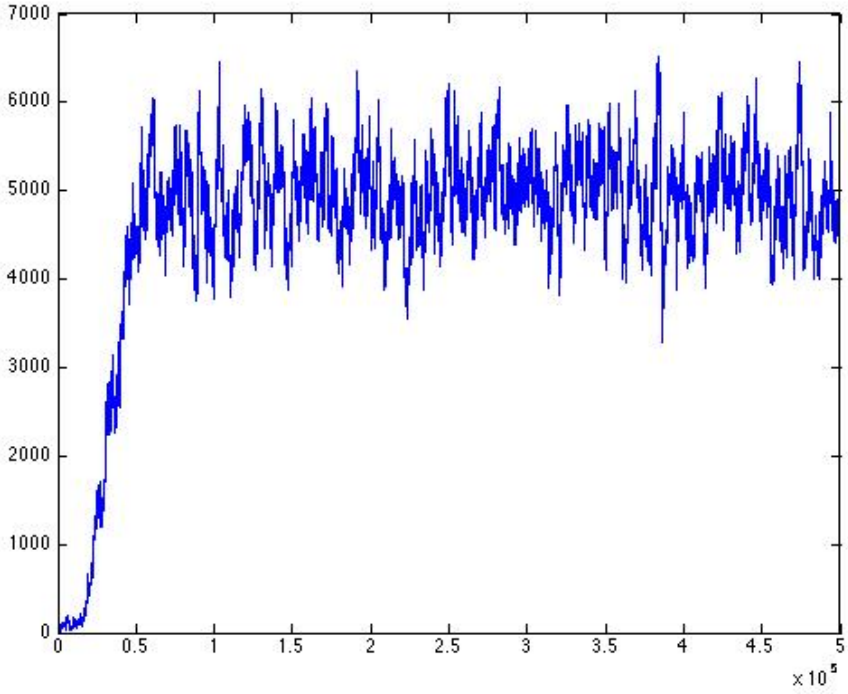
Doves	Hawks
	
t = 40,000	t = 40,000
	
t = 50,000	t = 50,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.18: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawks diffuse into the grid. Hawks persist at low levels on a substantial background Dove population.

Hawks



Doves

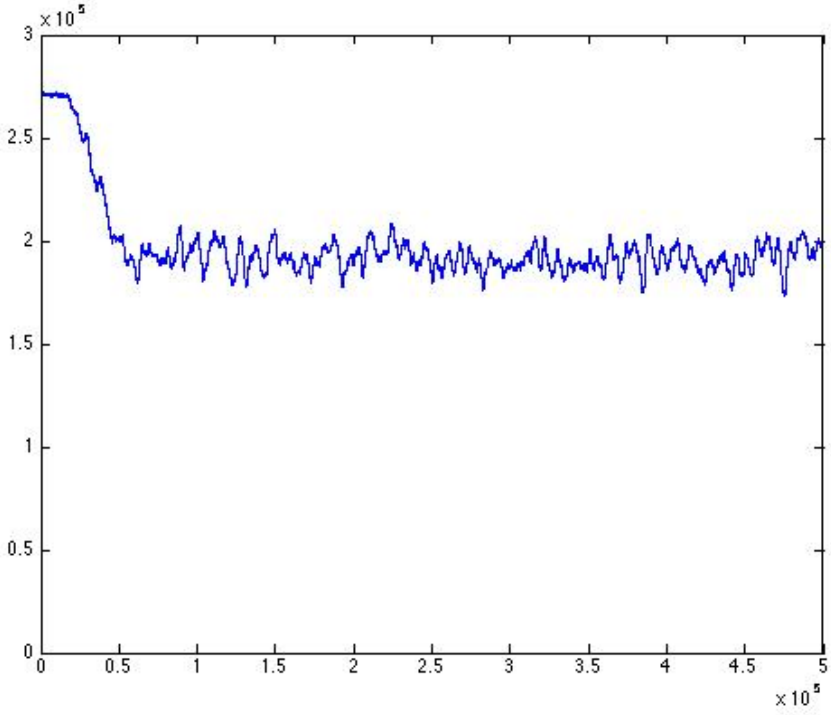


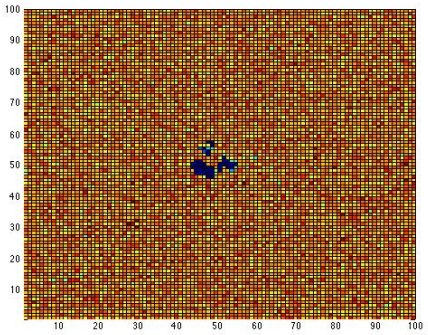
Table 6.19: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a low level of 4,631 individuals, 2.3% of the population. The Hawk population standard deviation was 1,198, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 197,080 individuals with a standard deviation of 19,351.

Non-Averaged Payoff Structure Without Kairomone Secretion

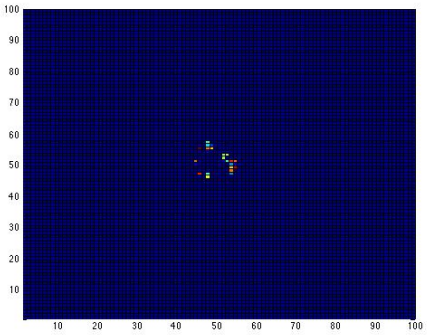
The advancing wavefront nature of invading Hawks that was evident in previous simulation was not present in this case. Rather the Hawks gradually percolated into the population in an uneven advance. The Doves appear to be evenly distributed over much of the grid, punctuated by numerous small regions in which the Hawks are active. The Hawk population persists at a relatively low level with an average over five hundred thousand timesteps of 7,485 individuals, representing 3.8% of the population. The Dove population at 190,200 individuals, shows only highly localised depletion due to the presence of the Hawks.

Doves

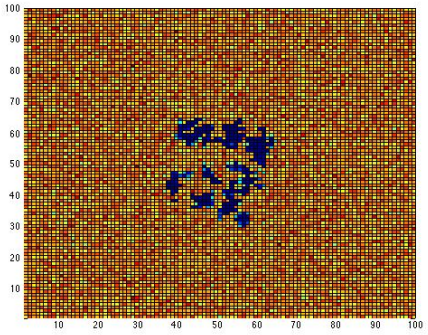
Hawks



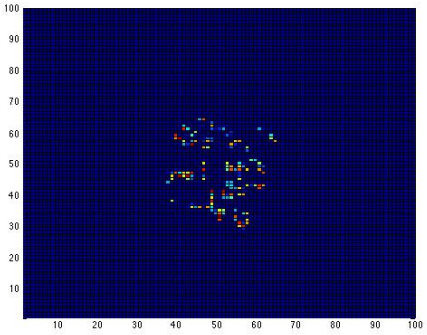
t = 3,500



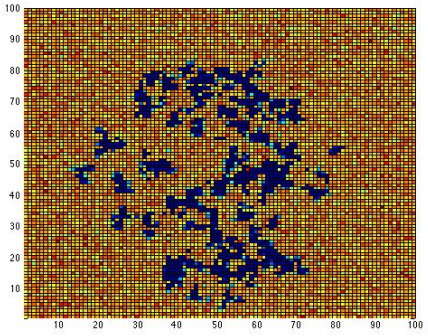
t = 3,500



t = 10,000



t = 10,000



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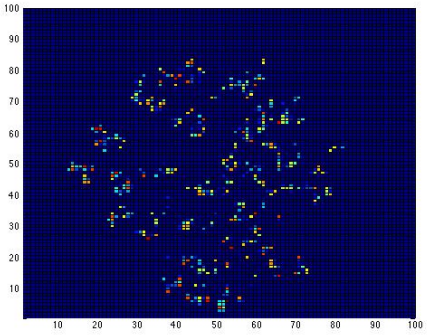
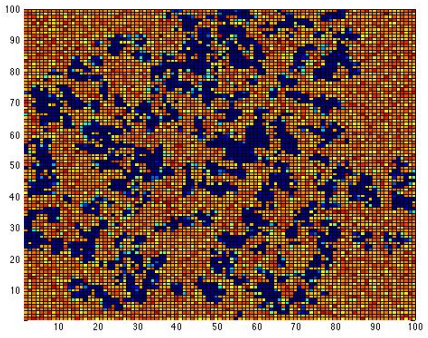
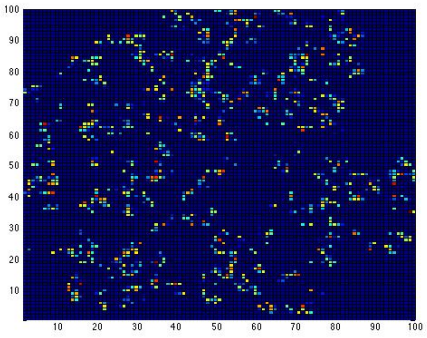


t = 20,000



t = 30,000



t = 30,000

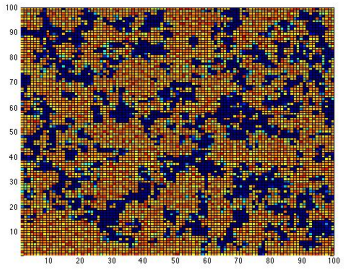
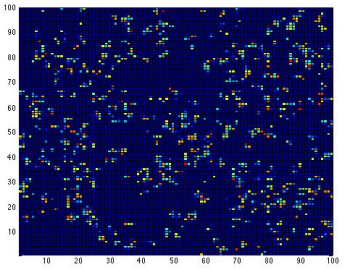
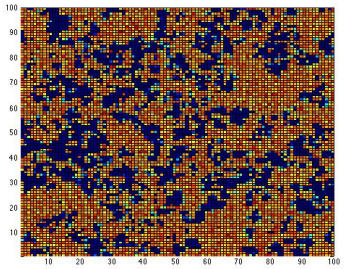
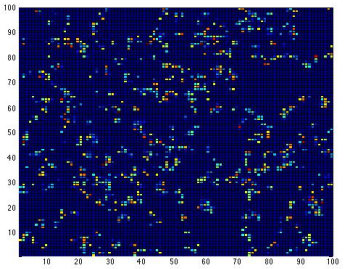
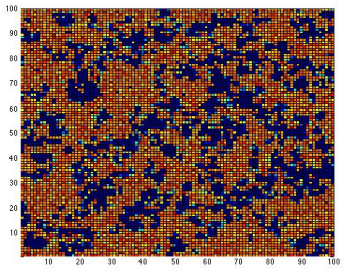
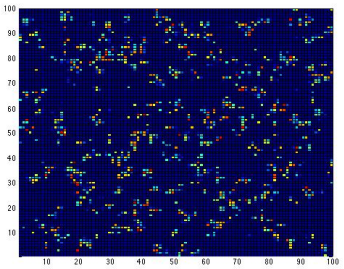
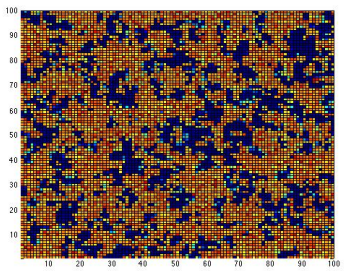
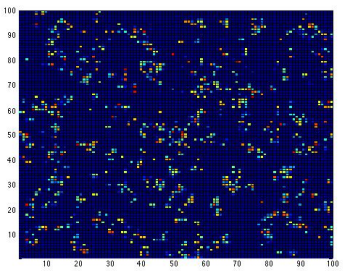
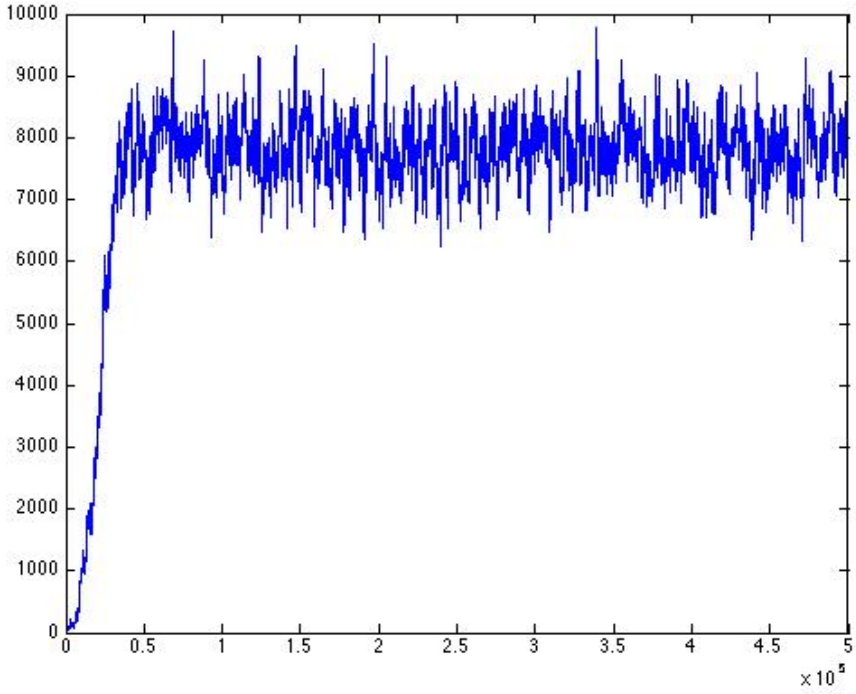
Doves	Hawks
	
t = 40,000	t = 40,000
	
t = 50,000	t = 50,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.20: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawks diffuse into the grid. Hawks persist at low levels on a substantial background Dove population.

Hawks



Doves

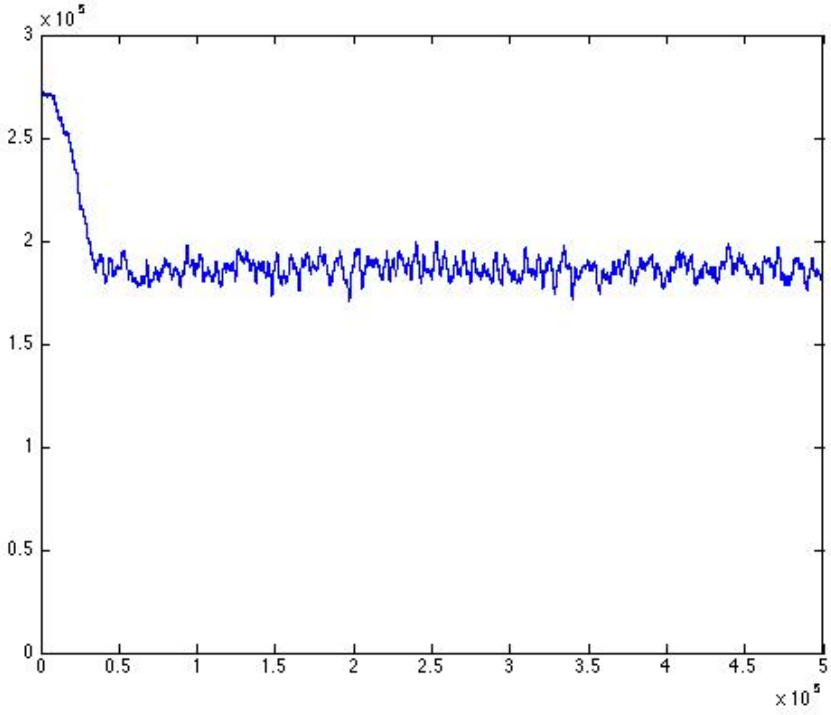


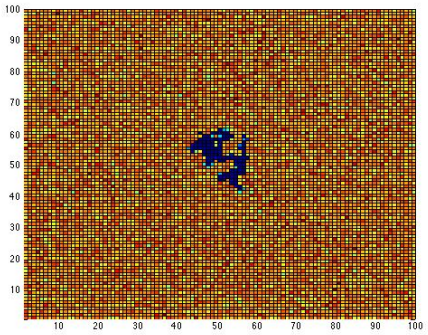
Table 6.21: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a low level of 7,485 individuals, 3.8% of the population. The Hawk population standard deviation was 1,470, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 190,200 individuals with a standard deviation of 162,980.

Non-Averaged Payoff Structure With Kairomone Secretion

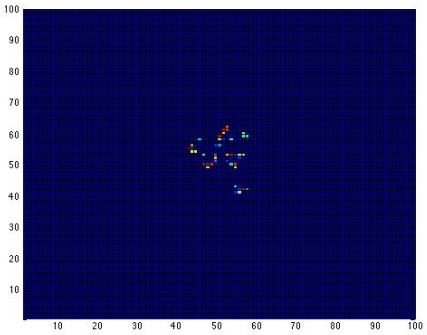
The advancing wavefront nature of invading Hawks that was evident in previous simulation was not present in this case. Rather the Hawks gradually percolated into the population in an uneven advance. The Doves appear to be evenly distributed over much of the grid, punctuated by numerous small regions in which the Hawks are active. The Hawk population persists at a relatively low level with an average over five hundred thousand timesteps of 5,106 individuals, representing 2.6% of the population. The Dove population at 189,710 individuals, shows only highly localised depletion due to the presence of the Hawks.

Doves

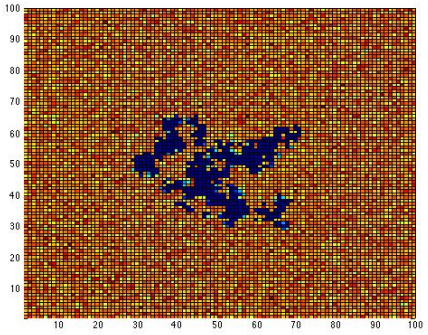
Hawks



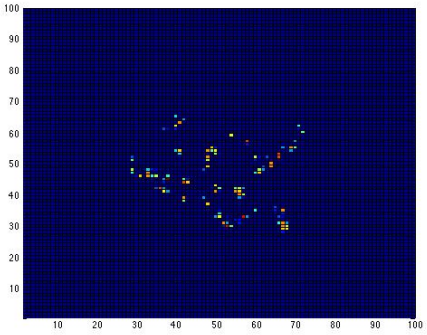
t = 3,500



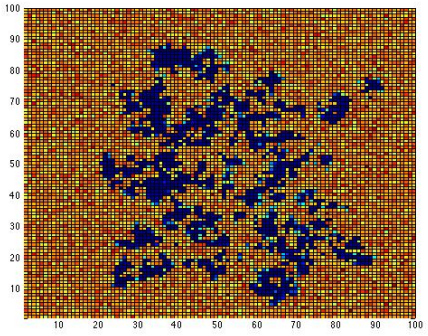
t = 3,500



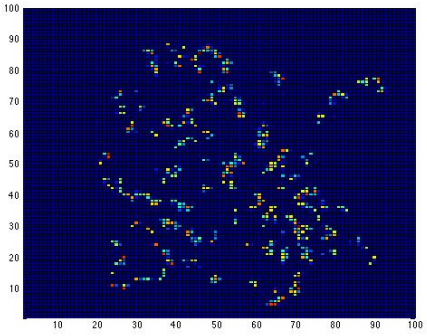
t = 10,000



t = 10,000



t = 20,000



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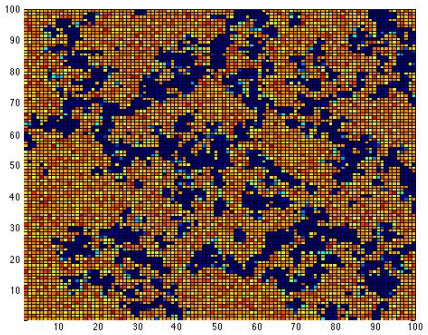

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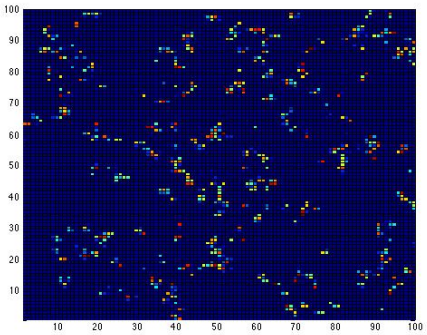


t = 30,000

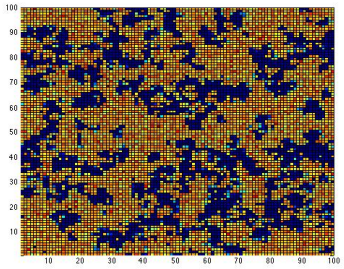
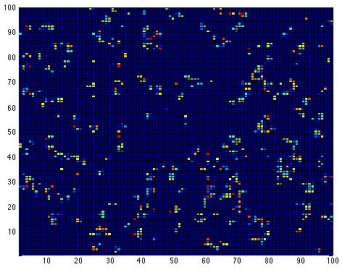
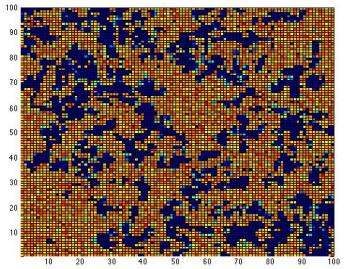
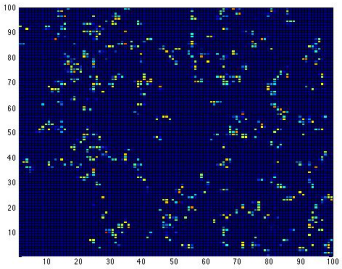
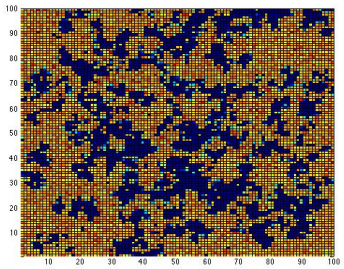
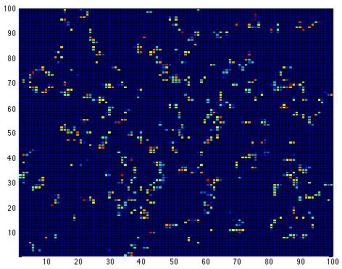
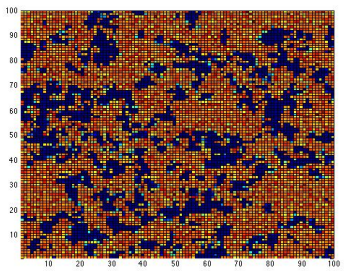
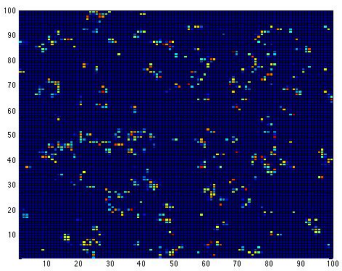
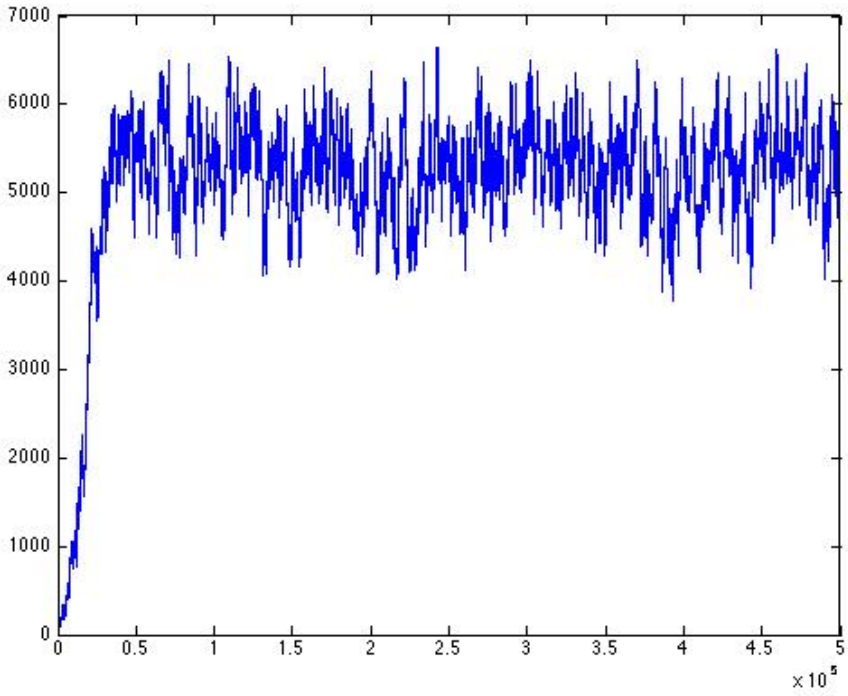
Doves	Hawks
	
t = 40,000	t = 40,000
	
t = 50,000	t = 50,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.22: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawks diffuse into the grid. Hawks persist at low levels on a substantial background Dove population.

Hawks



Doves

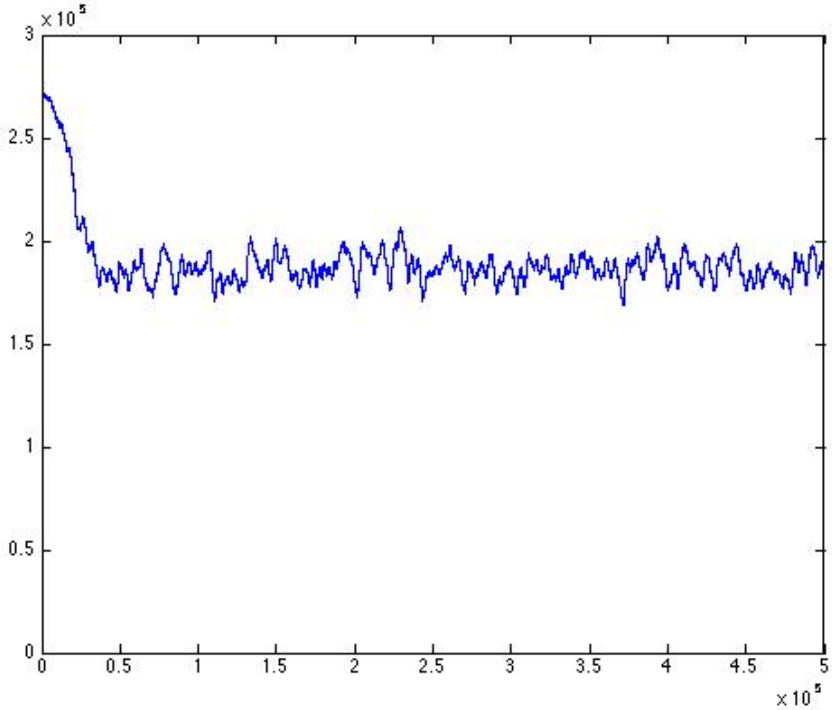


Table 6.23: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a low level of 5,106 individuals, 2.6% of the population. The Hawk population standard deviation was 961, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 189,710 individuals with a standard deviation of 15,548.

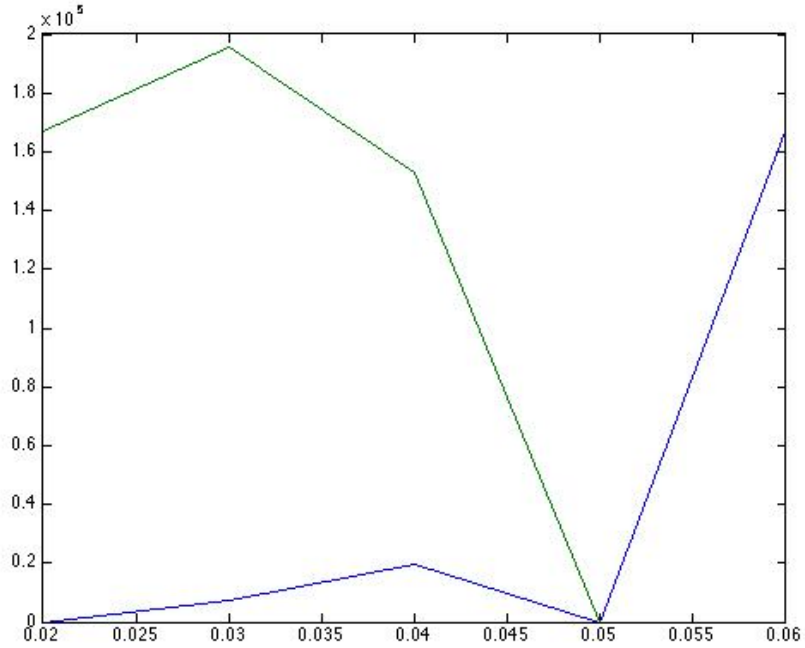
The Effect of Varying V

In this section we keep the cost of injury C constant at C = 0.03 and investigate the effect of varying the reward V on the population dynamics for each of the four simulation regimes.

Averaged Payoff Structure Without Kairomone

It was found that there was a relatively narrow range of values of V over which long term coexistence could be observed. For small values of V, in the range $V \leq 0.02$, for which the cost of injury exceeded the reward payoff, the Hawks generally became extinct, as one might expect. For large values of V, in the range $V \geq 0.06$, the population was all Hawks and the Doves became extinct. For the parameter range in between the situation is more complicated and more interesting. Extinction of both populations was observed for $V = 0.05$, ostensibly because the Hawks became very efficient at suppressing dove numbers but were unable to gain sufficient accumulated payoff from Hawk-Hawk interactions to leave a sustainable number of offspring. This occurs right on the cusp of the value of V for which the Hawks are able to take over the entire population, forcing the Doves into extinction and being able to survive on the strength of the mutual Hawk-Hawk interactions.

Population as a Function of V



Percentage Population Composition as a Function of V

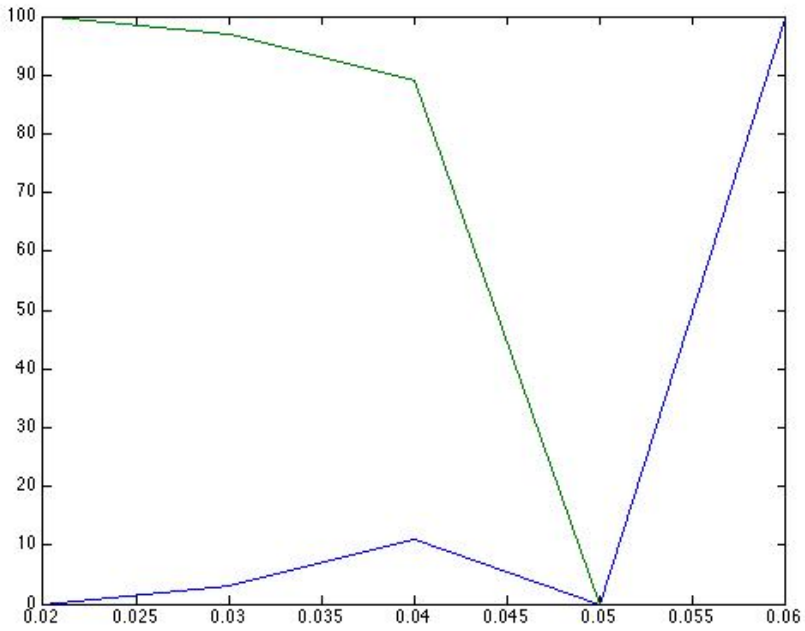
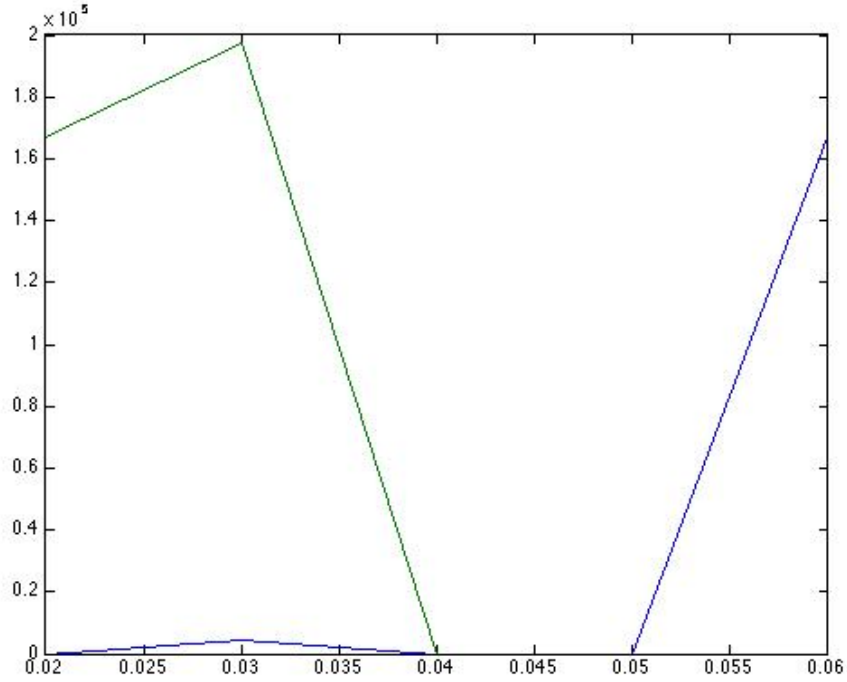


Table 6.24: The case of no kairomone secretion. The general trend is that as V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population. However note the mutual extinction event at $V = 0.05$, just before we reach a value of V for which the Hawks take over.

Non-Averaged Payoff Structure Without Kairomone

Varying V in the presence of a kairomone for the individual payoff structure it becomes clear that the kairomone is acting to destabilise the range of coexistence. Again the situation that, starting from a configuration of 4,999 Doves and one Hawk, the population develops to a stable state as all Doves for $V \leq 0.02$ and all Hawks for $V \geq 0.06$. At $V = 0.03$ there was observed coexistence, but the Hawks constituted a feeble if stable minority in a population composed overwhelmingly of Doves. Increasing the value of V did not lead to an increasing stable minority population of Hawks, but rather to the extinction of both populations. In fact extinction was observed for $0.04 \leq V \leq 0.05$. To some extent this may have been an artefact of the starting conditions. Perhaps different starting conditions and admixtures of strategy types may have resulted in a stable coexistence of types. As the number of different starting configurations is extremely large, regretfully we did not have sufficient time to explore this factor in the present work.

Population as a Function of V



Percentage Population Composition as a Function of V

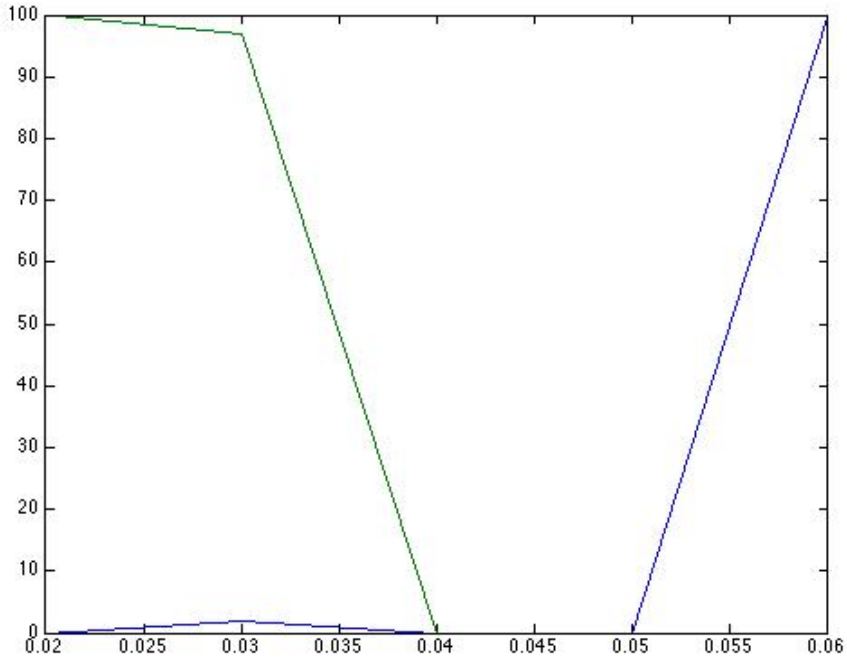
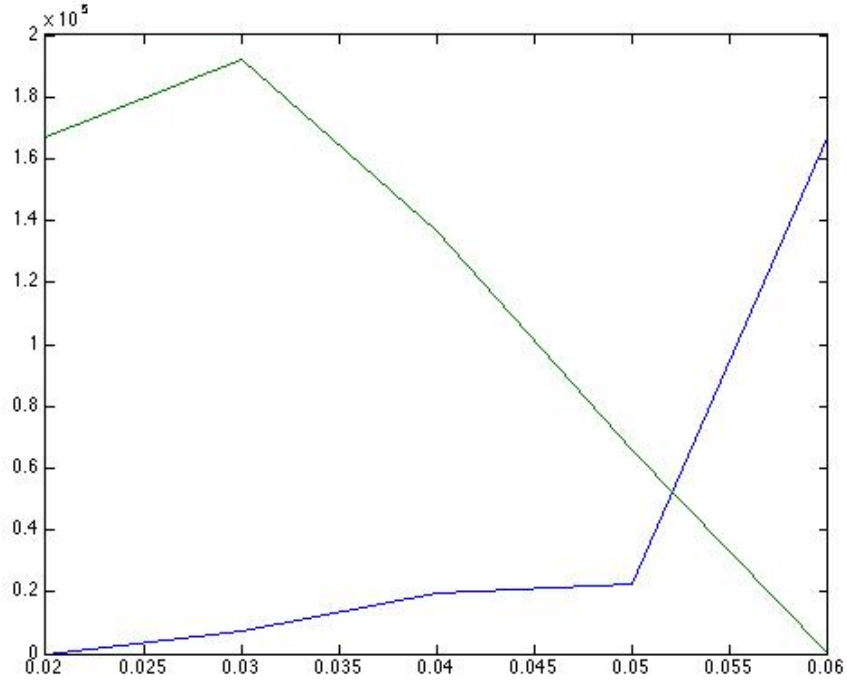


Table 6.25: The case with kairomone secretion. In the range intermediate between all doves and all Hawks, there is ether weak coexistence or more often, extinction of both population.

Averaged Payoff Structure Without Kairomone

This case gave rise to some of the most interesting behaviour in the non-synchronous Hawk-Dove simulations investigated here. As is already clearly a feature of these simulations, from our standard starting configuration, we observed a long term stable population of Doves result for $V \leq 0.02$ and a long term stable monomorphic population of hawks for $V \geq 0.06$. For all intermediate values of V we observed stable coexistence. As the value of V increases, the population of Hawks also increases until there is a rapid rise in Hawk numbers as we approach the value $V = 0.06$ where the Hawks become monomorphically stable. In fact for the simulation with $V = 0.05$ mutual extinction almost resulted. This was avoided only because a small residual mixed population managed to survive and expand to re seed the entire grid. In this case, interesting spiral wave like structures were observed. This case is presented in more detail in a subsection below. Typically for other simulation sets in this series there was at least one value of V for which mutual extinction was observed.

Population as a Function of V



Percentage Population Composition as a Function of V

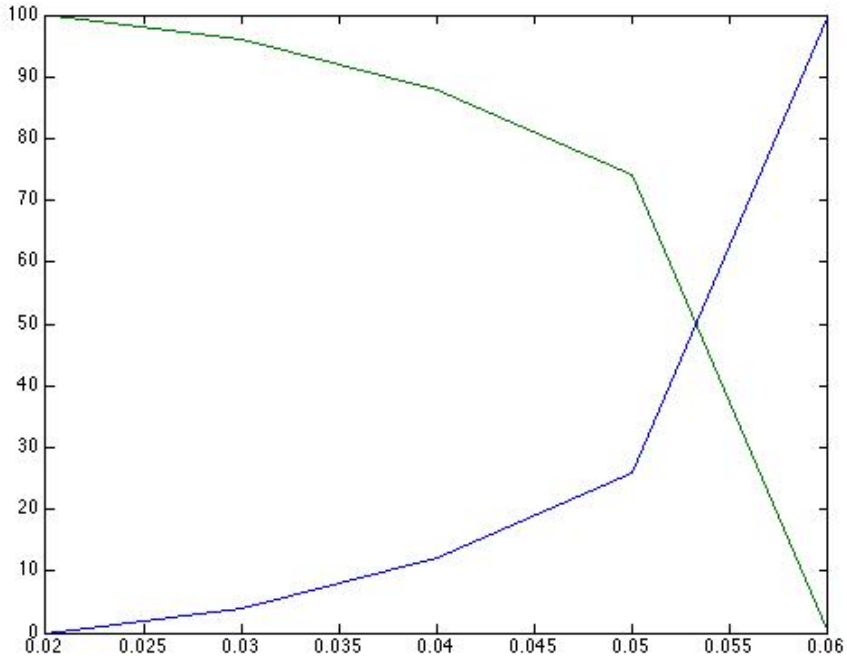
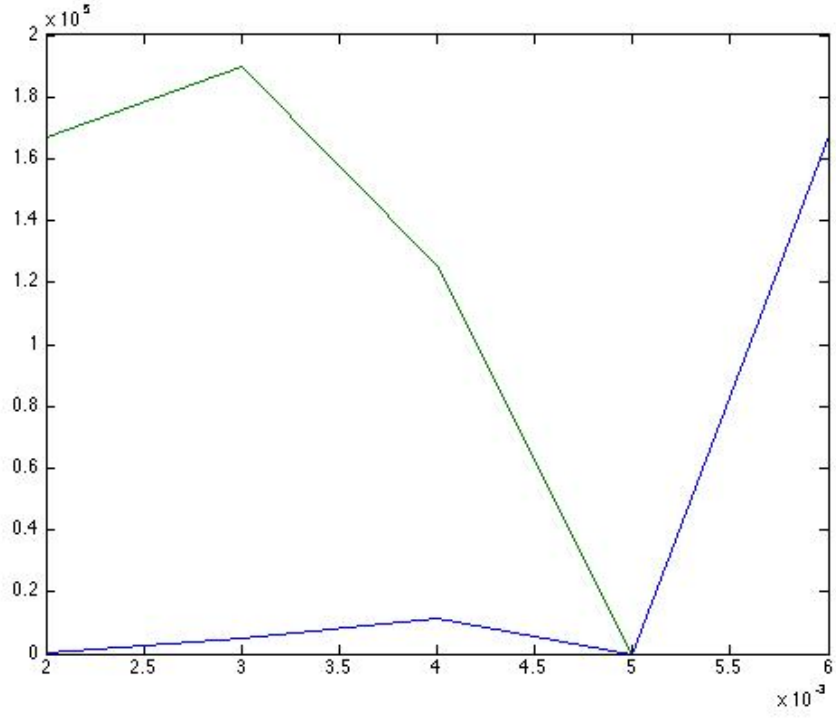


Table 6.26: The case of no kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

Non-Averaged Payoff Structure With Kairomone

Varying V in the presence of a kairomone for the individual payoff structure we find broadly similar behaviour to the previous case above. Coexistence was observed for the parameter range $0.02 < V < 0.05$, with the population being monomorphic in Hawks above this range and in Doves below this range. However, in this overlap region the population of Hawks is generally much lower than for the cases considered above. The change over from majority Dove to majority Hawk population was altogether much more rapid. Hawks actually became extinct in one of the simulations in this intermediate parameter range, illustrating how the low level of the Hawk population was particularly susceptible to chance extinction due to an unfavourable spatial configuration.

Population as a Function of V



Percentage Population Composition as a Function of V

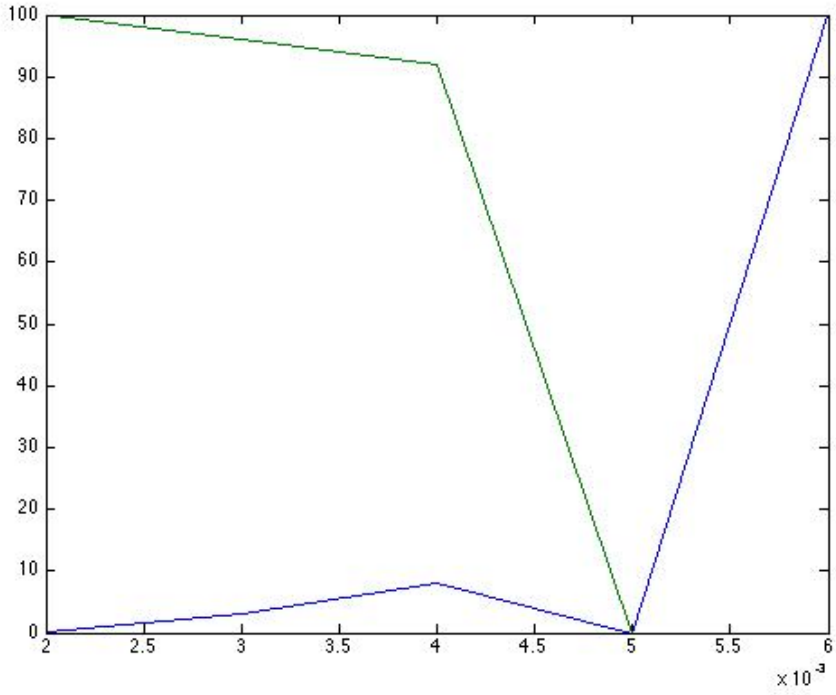


Table 6.27: The case with kairomone secretion. As V increases from its minimum possible value of 0.02, the Hawk population increases to form a stable minority in a background Dove population As V increases further the Doves become extinct as the Hawks take over the population.

An Example of Hawk Dove Simulation with Spiral Waves

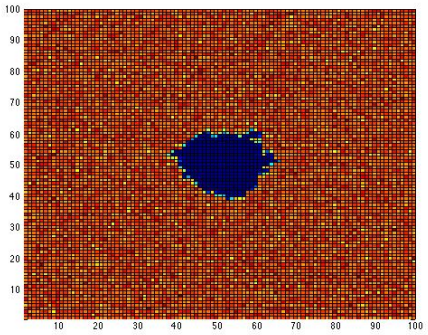
During the course of this group of simulations, the following case exhibited interesting behaviour. The game theory parameters were $V = 0.05$ and $C + 0.03$. The payoff structure is non-averaged and there was no kairomone secretion. The total average Hawk population over 5,000 time steps was 22,638 or some 25.6% of the total population. The Doves comprised an average of 65,596 individuals.

Unlike the above non synchronous cases, the Hawks did not 'percolate' into the surrounding Dove population. Rather the initial central Hawk gives rise to an advancing circular wavefront that advances through the Dove population leaving no survivors of either type except for a small colony at the bottom left hand corner of the grid. This remnant itself expands outwards in a near circular wavefront that breaks up into spirals and repopulates the grid with a dynamic pattern of spiral type wavefronts of Doves being chased by a similar shadow configuration of Hawks. This appears quite different to the spatial configuration of the the other non-synchronous simulations reported above and is more like one of he cases reported for the Prisoner's Dilemma.

This simulation also illustrates the importance of contingency or stochasticity in survival. By chance a small composite sub population had survived that was able to re populate the environment. The resulting population then exhibited a long term stability.

Doves

Hawks



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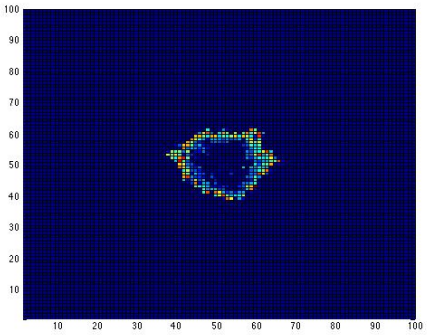
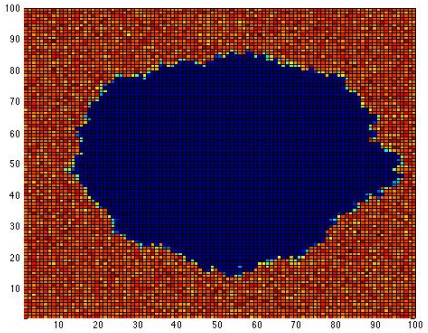


t = 3,500



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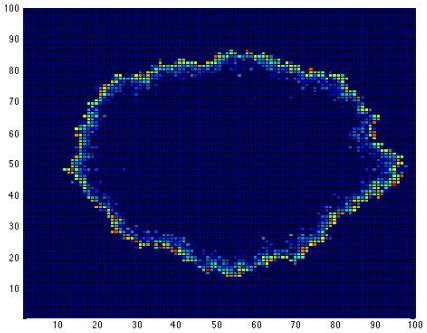

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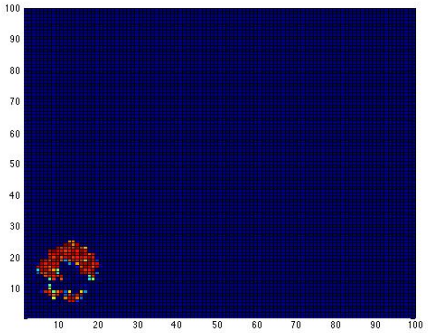

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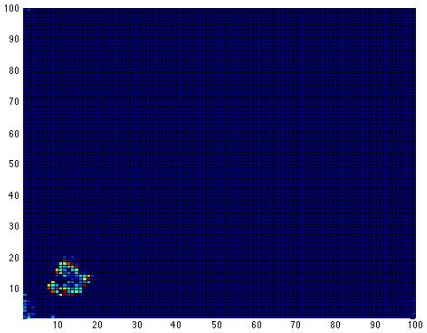

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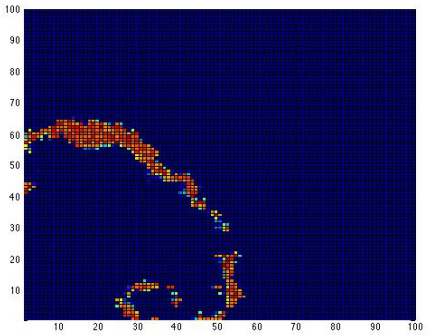

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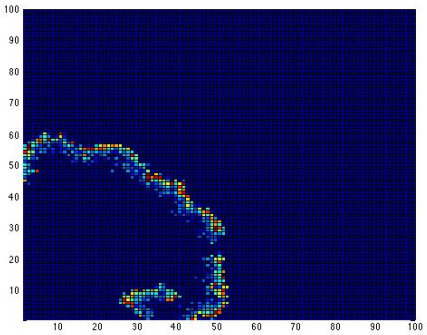


t = 30,000

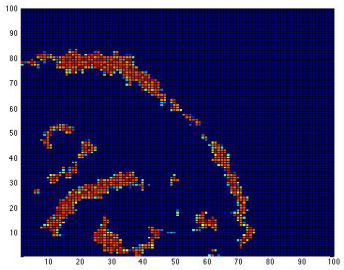
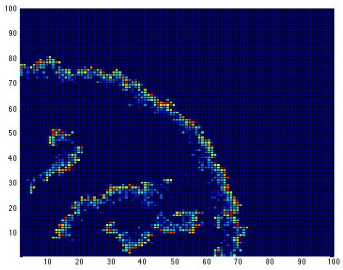
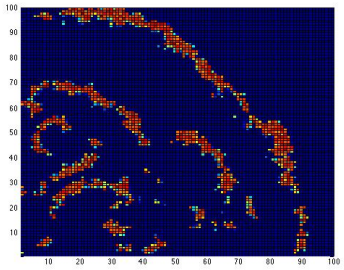
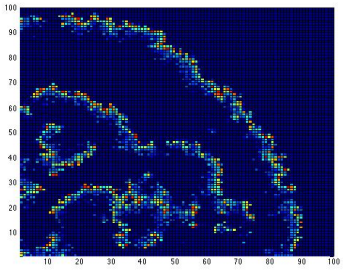
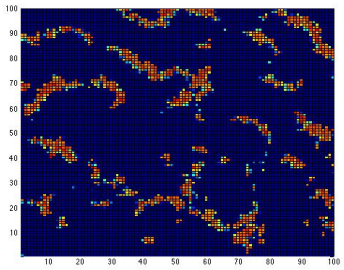
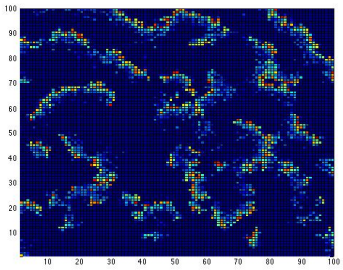
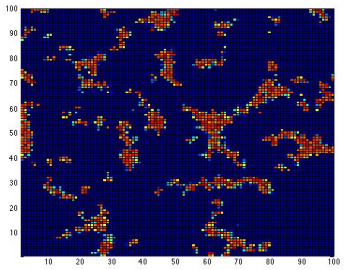
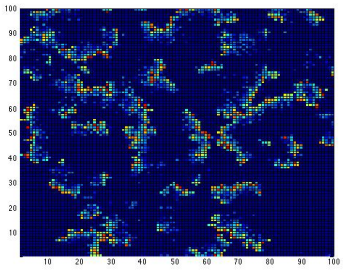
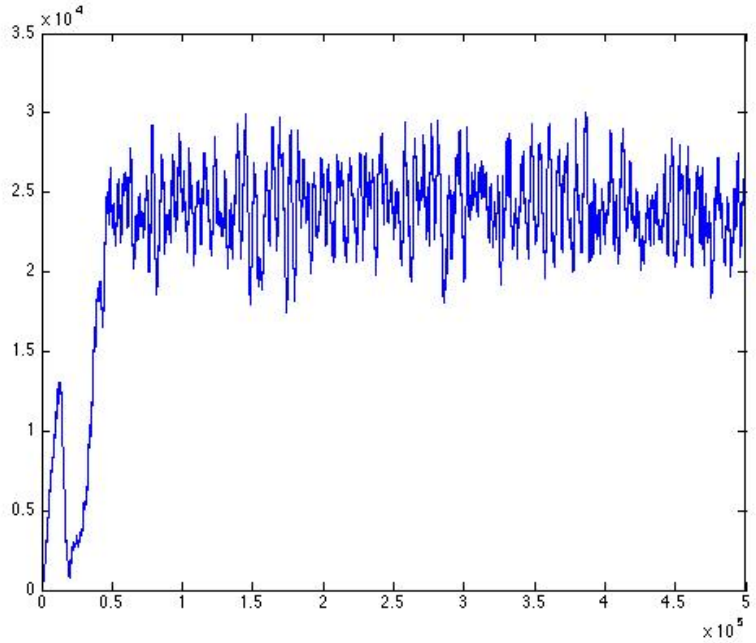
Doves	Hawks
	
t = 35,000	t = 35,000
	
t = 40,000	t = 40,000
	
t = 100,000	t = 100,000
	
t = 500,000	t = 500,000

Table 6.28: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is one Hawk at the centre of a grid surrounded by a random distribution of 49,999 Doves. Hawks diffuse into the grid. Hawks persist at low levels on a substantial background Dove population.

Hawks



Doves

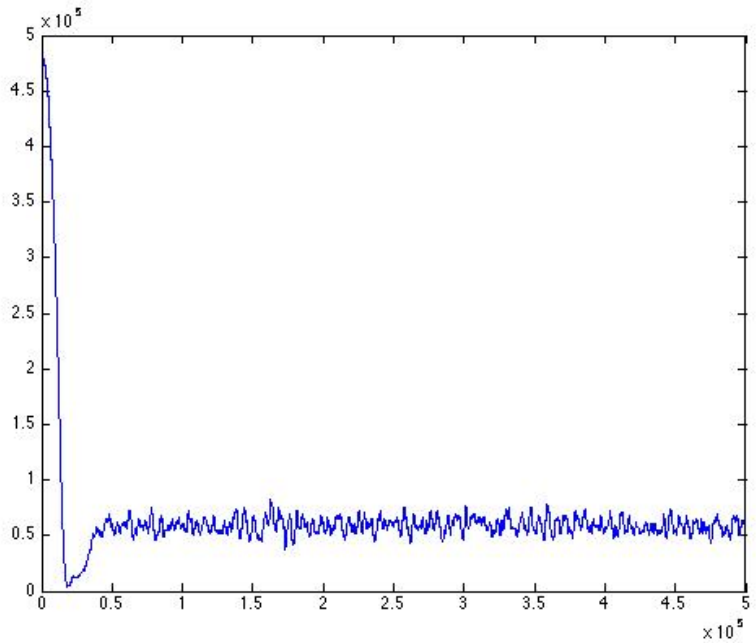


Table 6.29: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a level of 22,638 individuals, 25.6% of the population. The Hawk population standard deviation was 5,354, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 65,596 individuals with a standard deviation of 53,220. The dip in both plots indicated where both populations came close to extinction as the initial advancing Hawk wave reached the edge of the grid. The subsequent recovery led to long term stable averages for both strategy types.

Discussion

In this non-synchronous generation regime, all four simulation types had very much the same character. Unlike in the synchronous generation cases, the Hawks never form an advancing wavefront. Rather the Hawk population seems to diffuse into the surrounding Dove population, causing some localised depletion in Dove numbers. Consequently the Dove population persists at a very much higher level in the non-synchronous case than in the synchronous generation simulations, and it is comparatively less affected by the parasitism of the Hawks. Allowing the secretion of kairomone, and/or switching from an averaged to an individual payoff structure had relatively little effect on the population dynamics. Allowing kairomone secretion seems to cause a decrease in both populations, with Hawk populations reduced by some 30%. Changing from averaged to individual payoff structure had a relatively minor effect.

Table 6.30: Comparison of Simulation Results for Case $V = 0.04$, $C = 0.03$

Case	Payoff Structure	Kairomone (ν)	Hawk Mean	Dove Mean	Comment
1	Averaged	0	15,820 (28.4%)	39,853 (71.6%)	Coexistence
2	Not averaged	0	17,912 (24.8%)	54,352 (75.2%)	Coexistence
3	Averaged	1	21,118 (17%)	103,450 (83%)	Coexistence
4a	Not averaged	1	0	0	Extinction
4b	Not averaged	1	0	360,000	Doves survive

6.3 Mutations

Various mutation scenarios are possible. As in the Prisoner's Dilemma treated in the previous chapter, we may allow mutation of kairomone productivity, or kairomone sensitivity or of the strategies themselves. There are also manifold starting configurations to consider. Therefore a complete exploration of this aspect of these model ecologies is not possible, there being multitude of possible permutations of the above

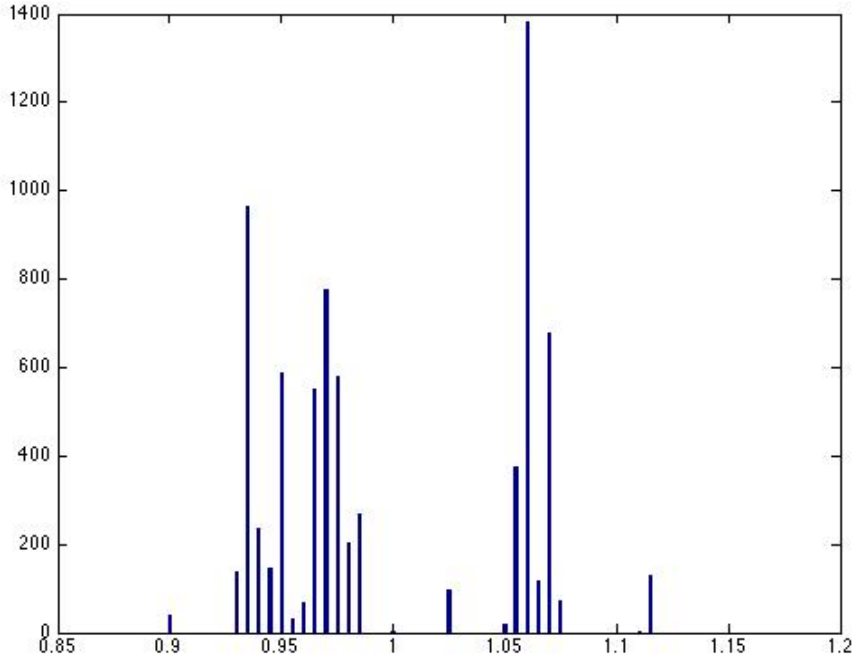
factors. Doubtless many interesting phenomena will be overlooked in the small initial summary presented below.

Mutation of Kairomone Productivity

Simulation 1

In the below simulation we allowed kairomone to mutate from a starting value of 1. The probability of mutation was 0.001 and the mutation amount (by which the kairomone productivity would be changed) was 0.005. A further extreme mutation of size 0.05 was allowed to occur with probability 0.0001. The starting configuration was that which is standard in the above, namely on Hawk at the centre of a population of 4,999 Doves. We used the individual payoff structure, in which in Hawk-Hawk contest a Hawk would have an equal chance of being allotted score V or $-C$, with the opponent being allocated the remaining score. We set the values of V and C to be 0.03 and 0.04 respectively. In this case the value of the resource is exceeded by the cost of injury, and the classical analysis based on the replicator equation leads to the expectation that the proportion of Hawks shoud be $\frac{V}{C} = \frac{3}{4}$. Generations were synchronous. The simulation was run for 1,200,000 time steps, after which time the distribution of the values for kairomone production were noted. These are shown in the plots below. The mean kairomone productivity of the Hawks and Doves remained close to their starting values, at 0.9980 and 0.9944 respectively. In the case of the Doves we might conclude that there was no significant selection pressure to change the value of the kairomone productivity, though mutations did cause this value to 'diffuse' to neighbouring values. For the Hawks, the population seems to have been fragmented into two sub populations, one with an average kairomone production below the starting value of 1, and another with value above 1.

Distribution of Kairomone Production Coefficients for Hawks



Distribution of Kairomone Production Coefficients for Doves

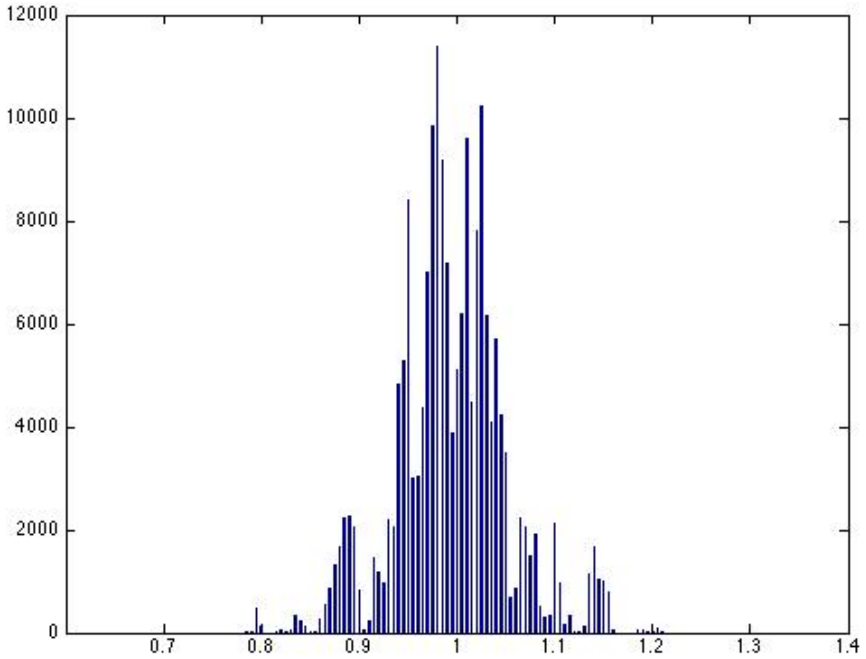
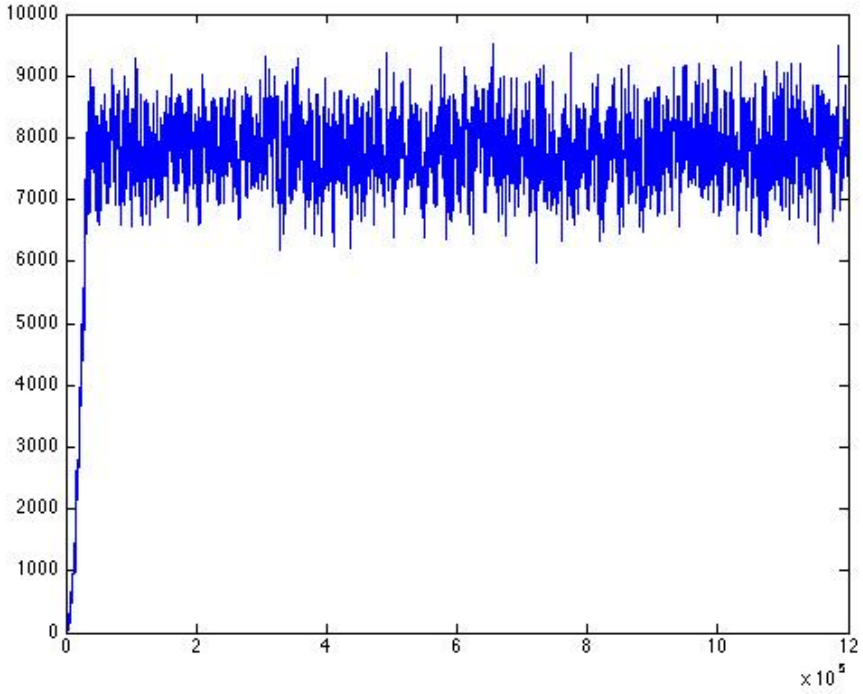


Table 6.31: These plots show the distribution of the kairomone production coefficients for Hawk and Dove agents after a period of 1,200,000 time steps starting from a configuration in which all such coefficients were set to unity.

Hawks



Doves

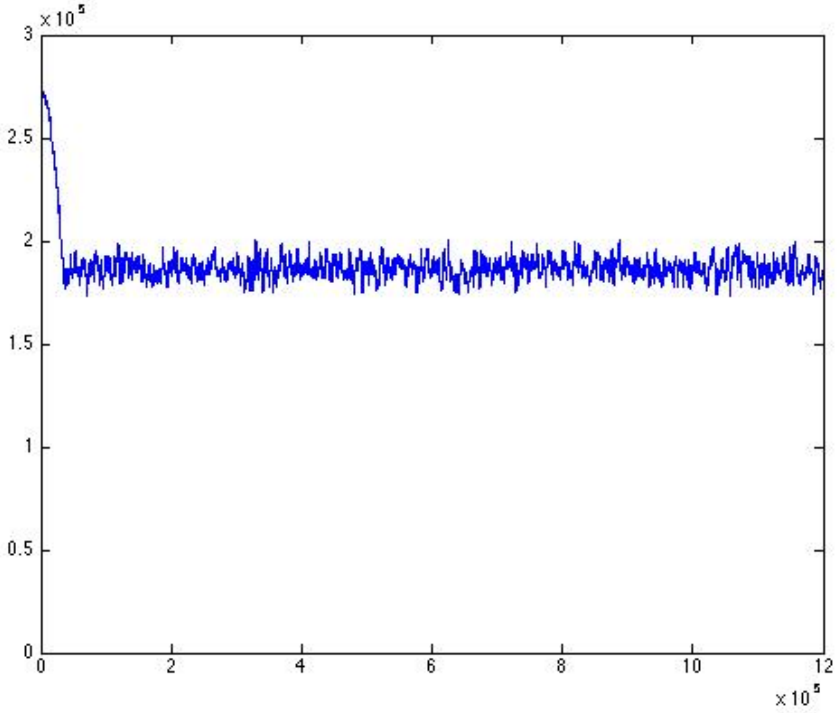
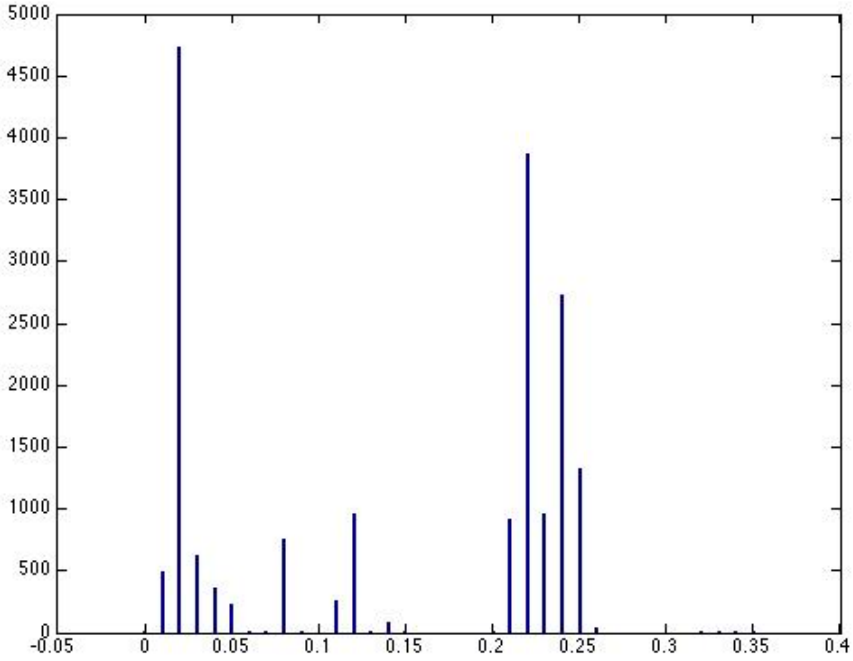


Table 6.32: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a low level of 7,050 individuals, 3.5% of the population. The Hawk population standard deviation was 1,417, showing that despite their low level the Hawks formed a stable minority. Doves averaged at 195,210 individuals with a standard deviation of 15,643.

Simulation 2

The game theory parameters V and C were the standard parameters as the last simulation. An averaged payoff structure was imposed and the generations were synchronous. The initial configuration was with zero kairomone production. Mutations in individual kairomone productivity occurred at reproduction. The mutation amount was set to be 0.01 with a probability of 0.001 with a further possibility of an extreme mutation by 0.1 with a probability of 0.0001. The simulation was run for two million time steps, representing approximately twenty thousand generations. Over this period there seemed to be a slight to moderate selection for increased kairomone secretion, with the pressure seemingly greater for the Hawks than for the Doves. At the simulation end, the mean value for the kairomone production parameter for the Hawks was 0.143, with a standard deviation of 0.097. The Dove production parameter was distributed about a mean of 0.077 with a standard deviation of 0.04. However, as the below population plots evince, there was no discernible effect of mutation on the long term population averages. To reveal such an effect a longer simulation, or a higher mutation rate would be required. Population levels remained similar to the case with zero kairomone secretion, as discussed in the first simulation results at the beginning of this chapter.

Distribution of Kairomone Production Coefficients for Hawks



Distribution of Kairomone Production Coefficients for Doves

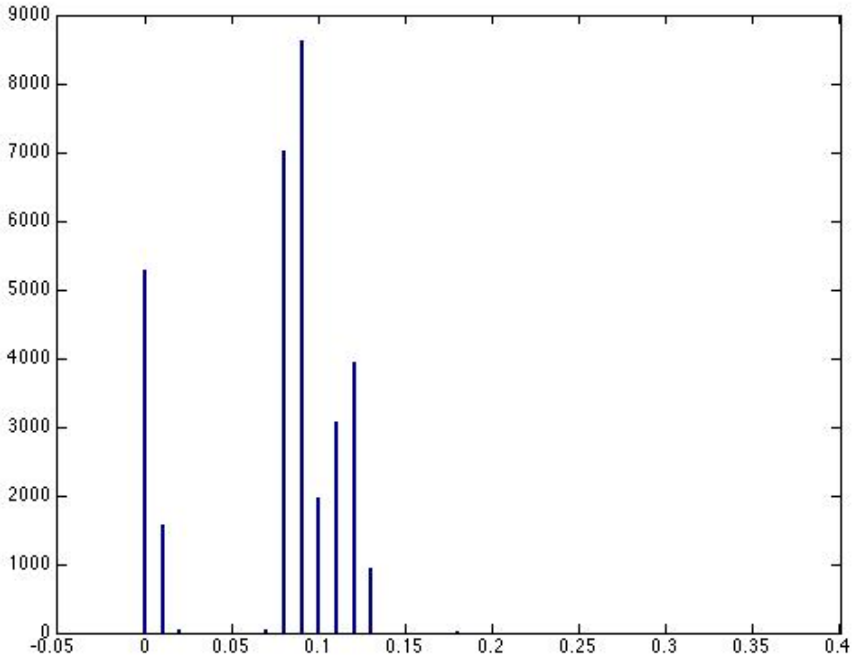
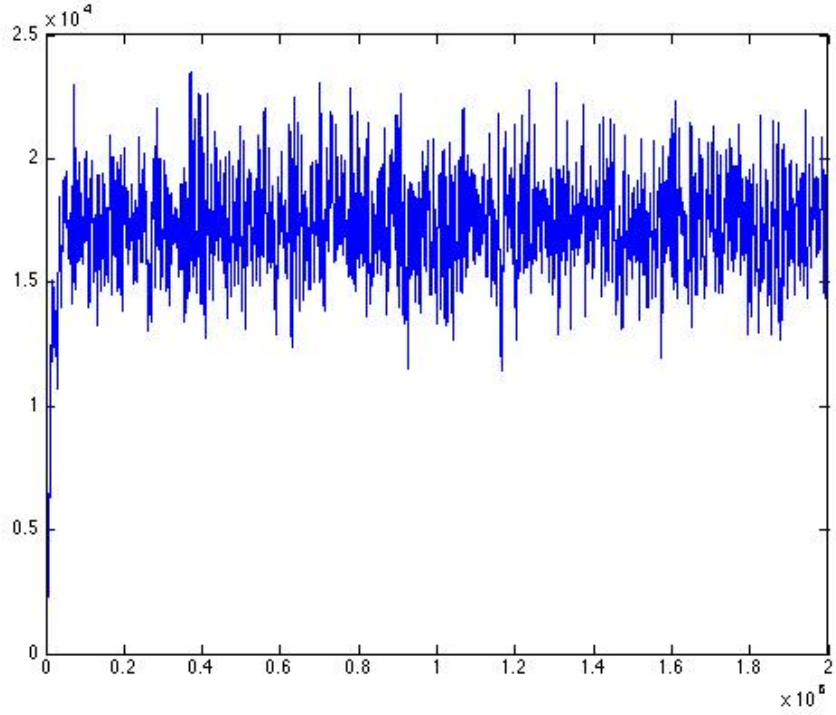


Table 6.33: These plots show the distribution of the kairomone production coefficients for Hawk and Dove agents after a period of 1,500,000 time steps starting from a configuration in which all such coefficients were set to zero.

Hawks



Doves

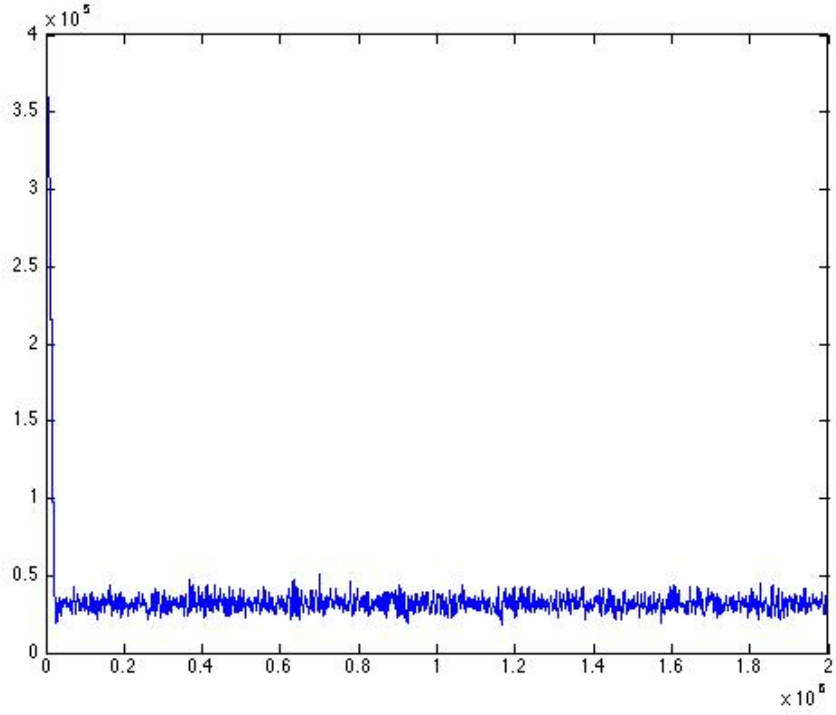


Table 6.34: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a stable minority level of 17,193 individuals, 33% of the population with a population standard deviation was 2,098. Doves averaged at 34,288 individuals with a standard deviation of 25,625

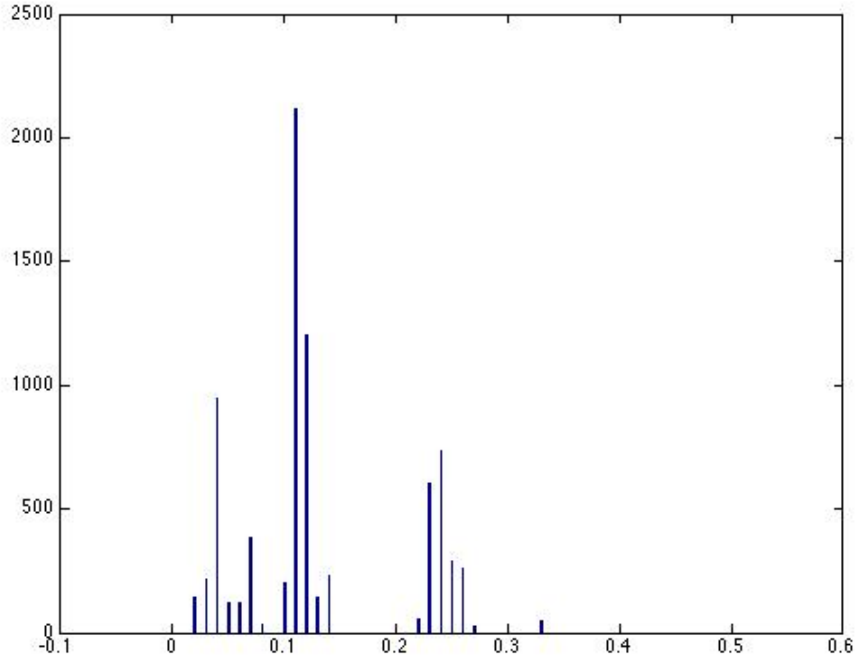
Simulation 3

This simulation was run with non synchronous generations. The game theory parameters were $V = 0.03$ and $C = 0.04$. An averaged payoff structure was used. Again the initial configuration was with zero kairomone production. Mutations in individual kairomone productivity occurred at reproduction. The mutation amount was set to be 0.01 with a probability of 0.001 with a further possibility of an extreme mutation by 0.1 with a probability of 0.0001. The simulation was run for one and a half million time steps, representing approximately fifteen thousand generations. Over this period there seemed to be a slight to moderate selection for increased kairomone secretion, with the pressure seemingly greater for the Doves than for the Hawks, which was a contrast to the previous simulation for the synchronous generation case.

The Hawks subsisted at a low level comprising an average of some 3.6% of the population, while the Doves remained by far the dominant component at 96.4%

At the simulation end, the mean value for the kairomone production parameter for the Hawks was 0.136, with a standard deviation of 0.0729. The Dove production parameter was distributed about a mean of 0.1415 with a standard deviation of 0.0901. Again, as the below population plots evince, there was no discernible effect of mutation on the long term population averages. To reveal such an effect a longer simulation, or a higher mutation rate would be required. Population levels remained similar to the case with zero kairomone secretion, as discussed in the first simulation results at the beginning of this chapter.

Distribution of Kairomone Production Coefficients for Hawks



Distribution of Kairomone Production Coefficients for Doves

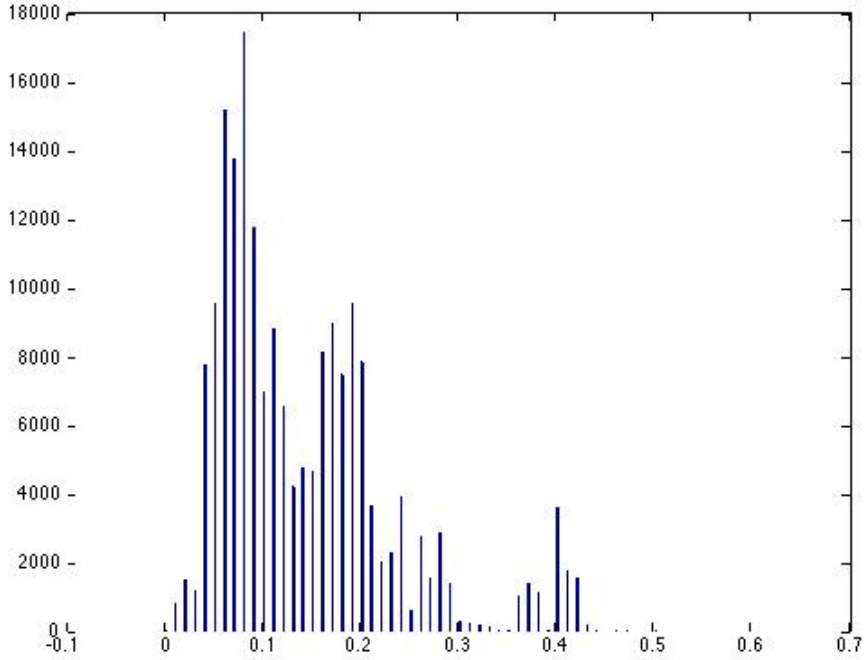
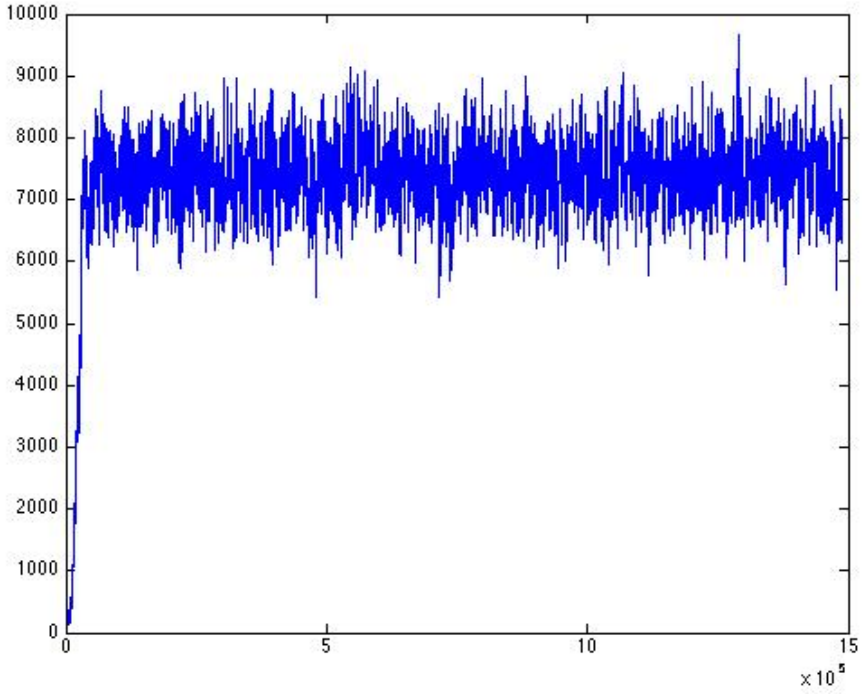


Table 6.35: These plots show the distribution of the kairomone production coefficients for Hawk and Dove agents after a period of 2,000,000 time steps starting from a configuration in which all such coefficients were set to zero.

Hawks



Doves

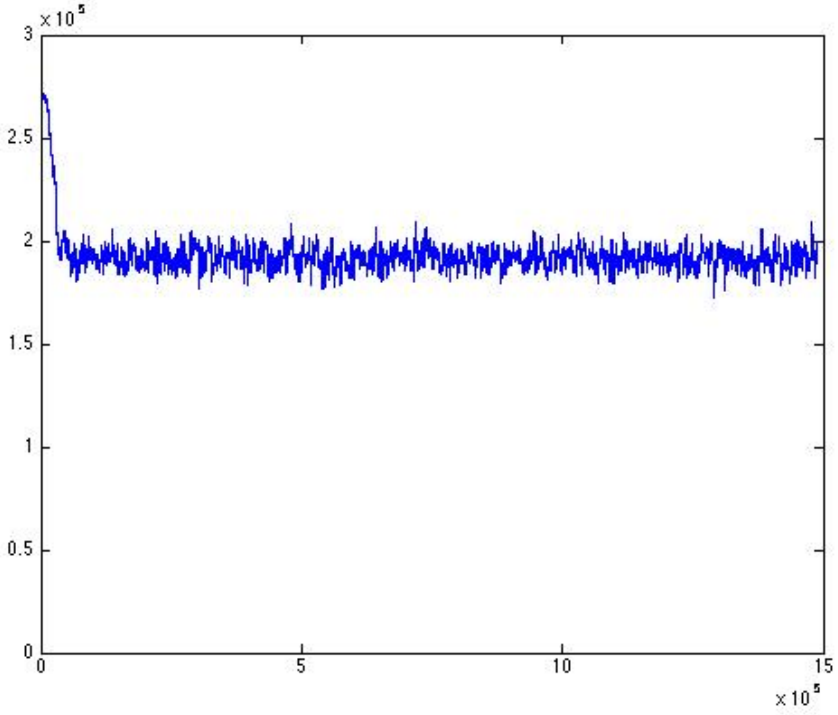
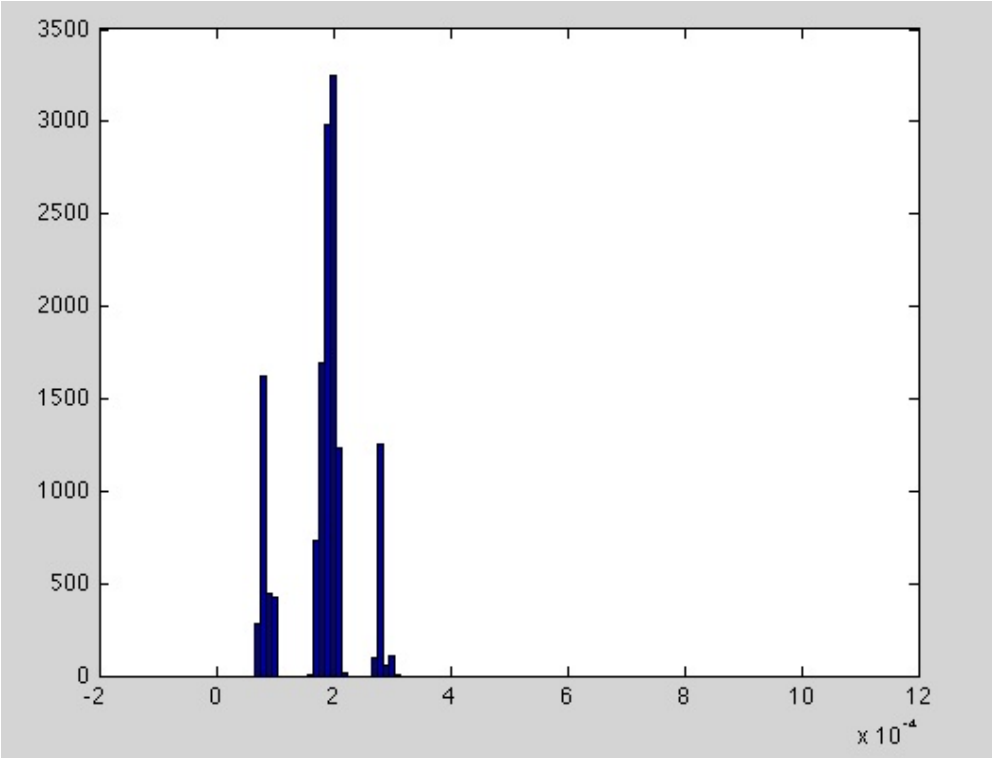


Table 6.36: Plots of the agent population in time. The Hawks gradually diffuse into the surrounding Dove population. Hawks persist at a stable minority level of 7,288 individuals, 3.6% of the population with a population standard deviation was 949. Doves averaged at 192,820 individuals with a standard deviation of 10,280.

Mutation of Kairomone Sensitivity

This simulation was similar to that described above in that the starting configuration was exactly the same, and the allowed mutation concerned the movement dynamics via the kairomone environment. Though in this case we allowed mutation in the agent sensitivity to kairomone rather than in its production. We start with all agents having the same standard kairomone sensitivity $\chi = 0.0002$, and kairomone productivity is unity as usual. The initial configuration is a single Hawk at the centre of a population of 4,999 Doves. We consider the individual payoff structure for this game, rather than the averaged payoff for Hawks in a Hawk-Hawk contest. Again there are two mutation schemes, a small mutation and a gross mutation. Small mutations in χ are of size 0.00001 and occur with probability 0.001. Gross mutations are of size 0.0001 and occur with probability 0.0001. Simulations were run for 1,200,000 time steps, after which time the distribution of values for χ was recorded. Population numbers were also recorded and plots of population versus time for each agent type were made. Unexpectedly, the Doves exhibited a sustained gradual decline in numbers throughout the course of this simulation. This is certainly due to the mutation in kairomone sensitivity, since simulations with the same parameters but without mutations so not exhibit such a decline. To proceed further it would be instructive to allow such simulations to run for longer in an attempt to see if a stable state is reached at some point, or whether the gradual decline observed is terminal and would eventually lead to the extinction of the Doves altogether.

Distribution of Kairomone Sensitivity Coefficients for Hawks



Distribution of Kairomone Sensitivity Coefficients for Doves

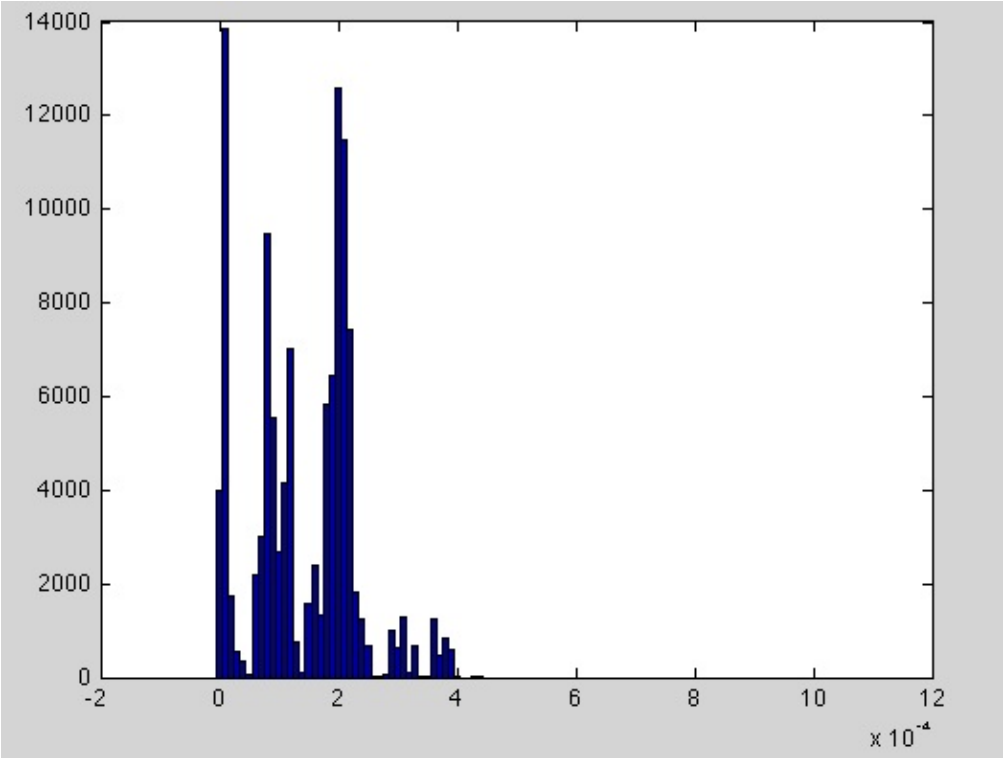
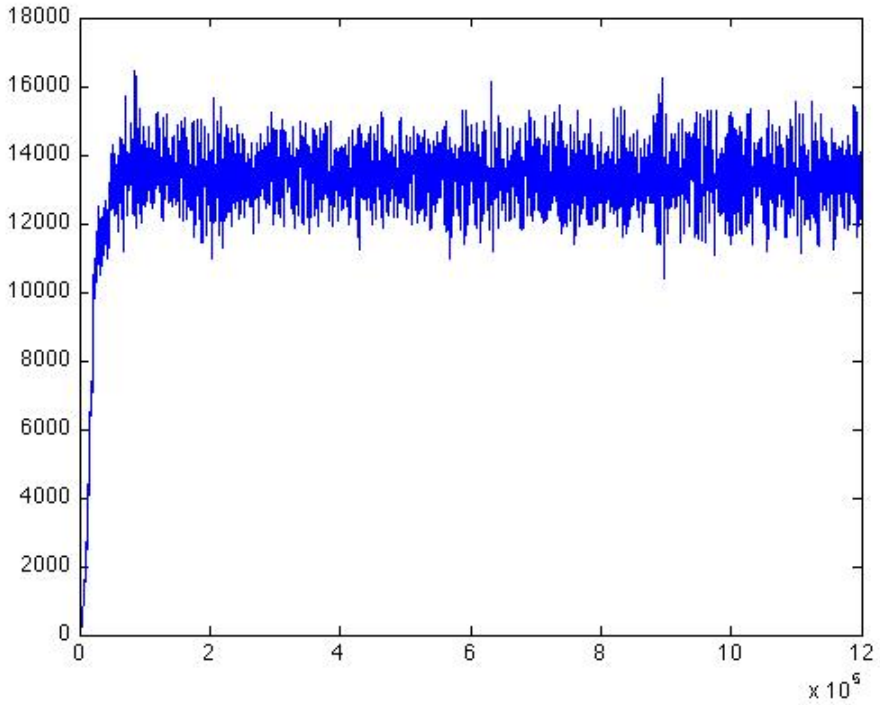


Table 6.37: These plots show the distribution of the kairomone sensitivity coefficients for Hawk and Dove agents after a period of 1,200,000 time steps starting from a configuration in which all such coefficients were set to the standard value for this thesis which was 0.0002.

Hawks



Doves

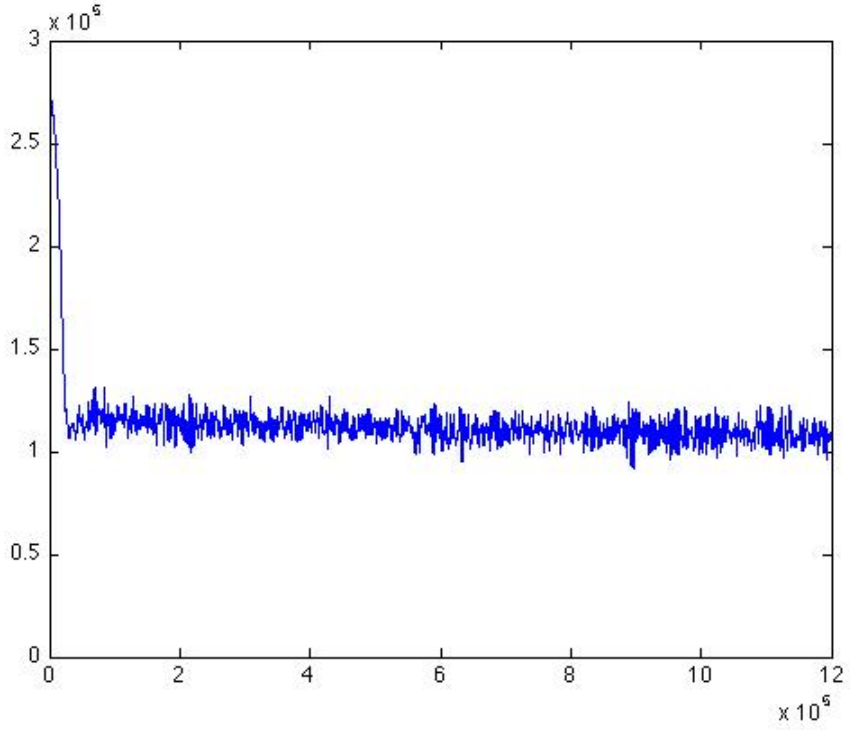


Table 6.38: Plots of the agent population in time. The Dove population seems to be on a slow but steady decline as the value of the kairomone sensitivity is allowed to mutate.

Mutation of Probabilities in Mixed Strategies

In this section we describe a simulation scenario in which we allow the strategies themselves to mutate. This is to say that we allot to agents a probability p of playing Dove during any particular encounter, and $1-p$ of playing Hawk. It is this probability that we allow to mutate. There are many possibilities for the mutation mechanism and also a vast parameter range available to explore in this simulation set up. We continue with the standard parameter range outlined above and investigate how behaviour is affected by various payoff parameters V and C. We start with a random spatial distribution of agents all of which are Doves , $p = 1$. The value of p is constant for an agents life time (100 time steps), but mutation can occur at reproduction when an agents offspring may be programmed with a different value of p to that of its parent. We set the probability of mutation to be 0.001, and the amount by which p mutates at each stage is set to be 0.1. This is to say that on average one in a thousand offspring at reproduction will differ from their parent in their value of the probability of playing Dove p by 0.1, and the rest will inherit their parental value of p. Thus as the simulation progressed the allowed values of p for each individual were the members of the set $\{0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0\}$.

In the following two simulations we set $V = 0.04$, $C = 0.05$ and we take results up to time step 2,000,000, which is to say that the simulation is run for 20,000 generations. We run the simulation with these parameters for both the averaged and the individual Hawk-Dove payoff structures and we set kairomone production to zero.

Simulation 1: Averaged Payoff Structure

The striking feature of this simulation is that a stable equilibrium is reached both in terms of the population level, which fluctuates about a stable equilibrium value, and

in terms of the value of p which similarly becomes established at a stable average value. The average population over the course of the simulation was 93,808 with a standard deviation of 22,256. This the population was stable. We can separate out plots for those agents that play mostly Dove ($p > 0.5$) and those that play mostly Hawk ($p < 0.5$). The number of agents playing mostly Hawk was 26,574 (28%), and the number playing mostly Dove was 67,234 (72%).

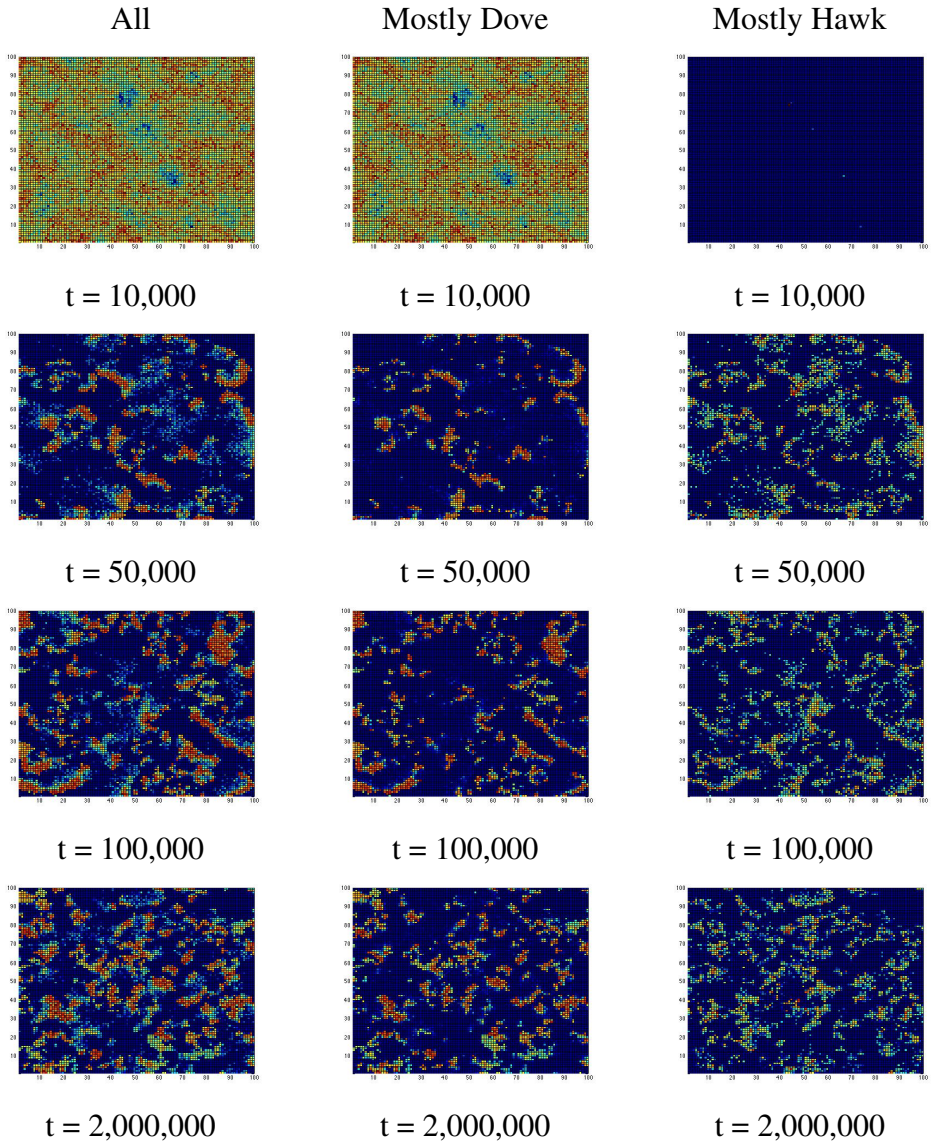
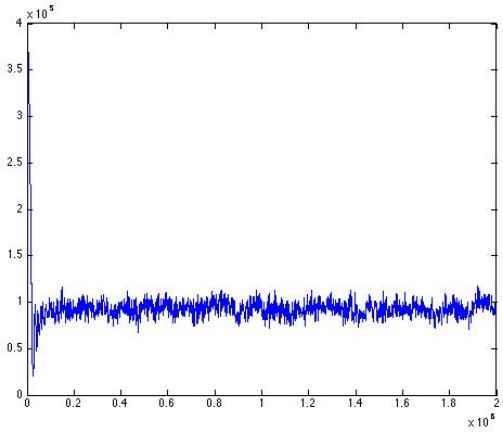
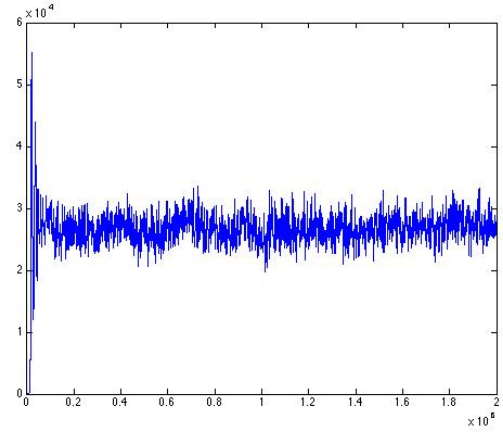


Table 6.39: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is for all agents to be Doves ($p = 1$).

All



Mostly Hawk



Mostly Dove

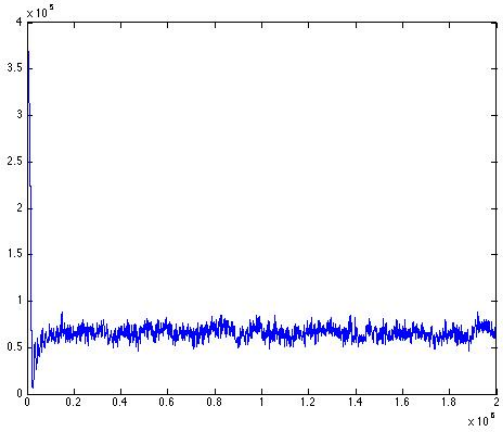
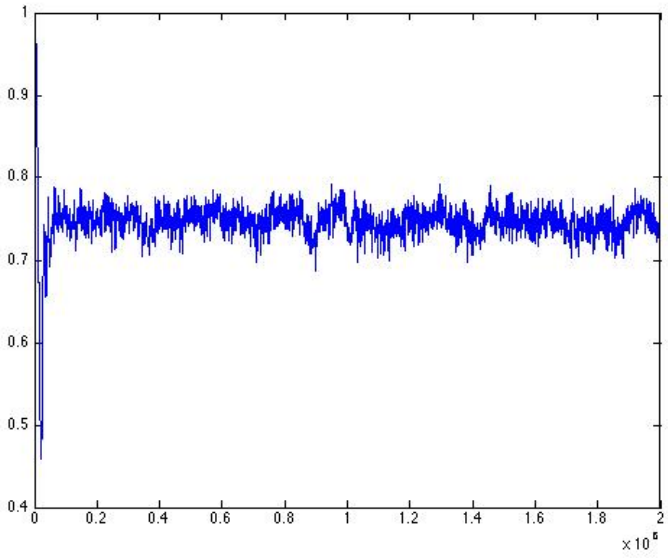


Table 6.40: Plots of the agent population in time. The populations exhibit fluctuations about a long term stable average.

As the probabilities are allowed to mutate between generations, a stable average value for p emerged naturally from the dynamics. The average value of p over the time of the simulation was 0.7462, with a standard deviation of 0.0274. Whilst the average value of p across the population at the last time step was 0.7436 with a standard deviation of 0.3333. From the population profile for the value of p at $t = 2,000,000$ it is clear that it is not the case that the average value of p is actually well represented in the population. Rather all values of p are represented and there is a very significant contingent of the population that are always Doves with $p = 1$, and another major fraction of the population which plays Dove with probability $p = 0.3$.

Time Series of Average Probability of Playing Dove



Population Profile of Probability of Playing Dove at Final Time Step

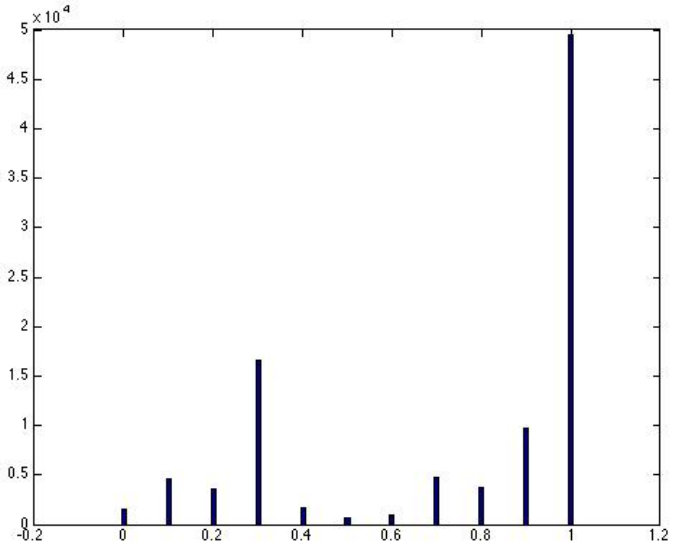


Table 6.41: These plots show the probability of playing Dove in the population. The first shows the evolution of the average for the population over the course of the simulation, and the second gives the population profile at the final simulation time step at $t = 2,000,000$.

Simulation 2: Individual Payoff Structure

Again a stable equilibrium is reached both in terms of the population level, which fluctuate about a stable equilibrium value, and in terms of the value of p which similarly becomes established at a stable average value. The average population over the course of the simulation was 98,185 with a standard deviation of 21,884. This the population was stable. We can separate out plots for those agents that play mostly Dove ($p > 0.5$) and those that play mostly Hawk ($p < 0.5$). The number of agents playing mostly Hawk was 28,119 (29%), and the number playing mostly Dove was 70,066 (71%).

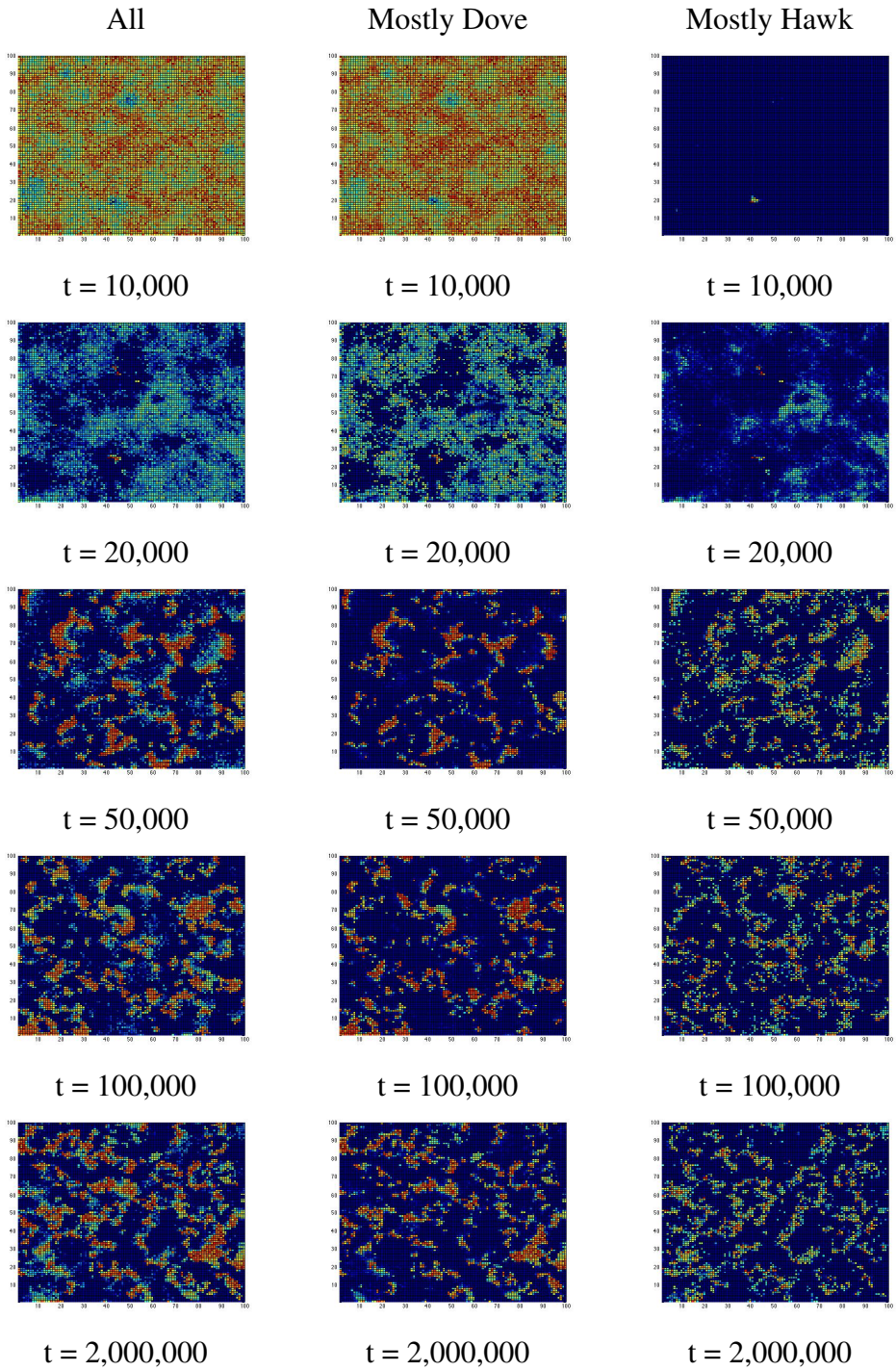
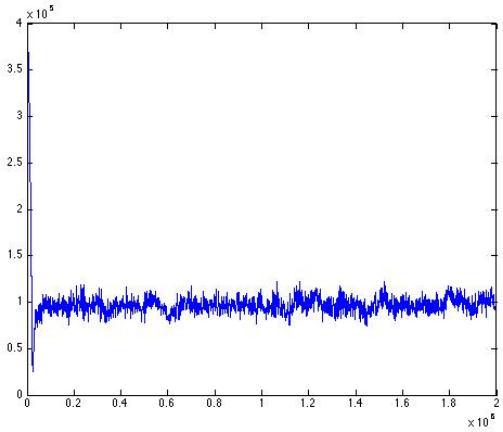
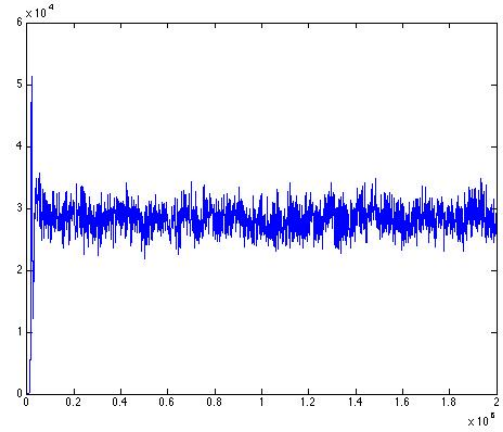


Table 6.42: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is for all agents to be Doves ($p = 1$).

All



Mostly Hawk



Mostly Dove

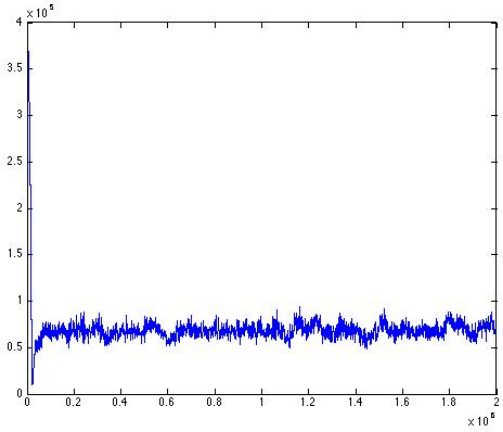
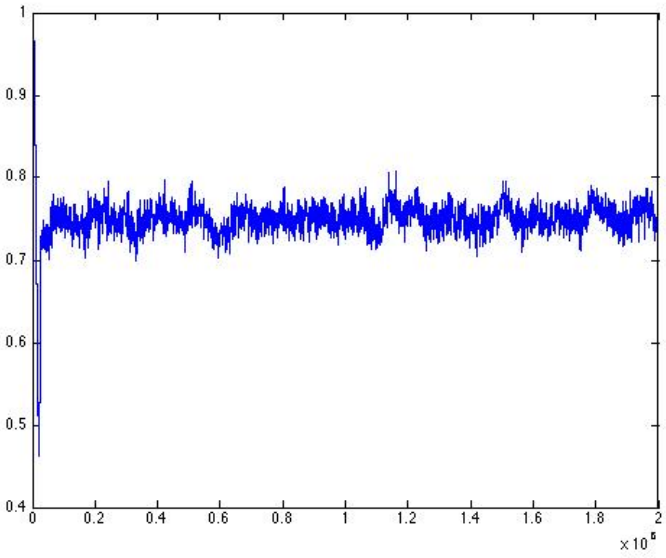


Table 6.43: Plots of the agent population in time. The populations exhibit fluctuations about a long term stable average.

As the probabilities are allowed to mutate between generations, a stable average value for p emerged naturally from the dynamics. The average value of p over the time of the simulation was 0.7503, with a standard deviation of 0.0260. Whilst the average value of p across the population at the last time step was 0.7468 with a standard deviation of 0.3365. From the population profile for the value of p at $t = 2,000,000$ it is clear that it is not the case that the average value of p is actually well represented in the population. Rather all values of p are represented and there is a very significant contingent of the population that are always Doves with $p = 1$, and another major fraction of the population which plays Dove with probability $p = 0.2$.

Time Series of Average Probability of Playing Dove



Population Profile of Probability of Playing Dove at Final Time Step

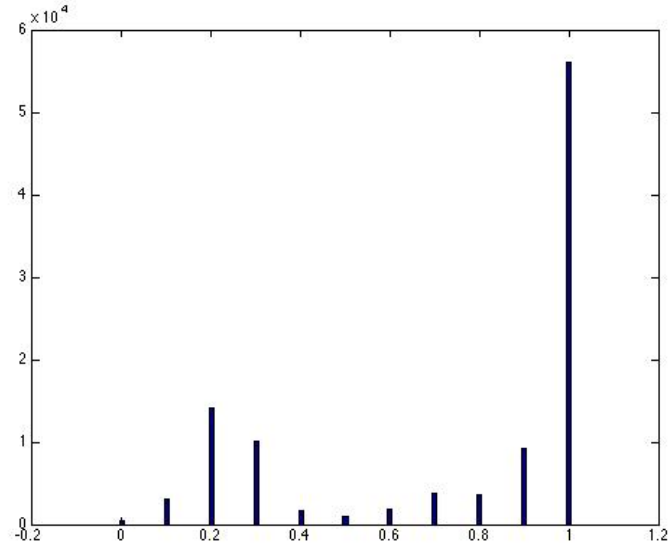


Table 6.44: These plots show the probability of playing Dove in the population. The first shows the evolution of the average for the population over the course of the simulation, and the second gives the population profile at the final simulation time step at $t = 2,000,000$.

Discussion

In both simulation cases, a stable population with a stable value for the probability of playing Dove p resulted. However, the populations were not static or monomorphic, and the emergent value of p was not well represented by any individual. Rather this value resulted from a range with representatives in the population at all values of p with the major contingent at $p = 1$ and the next significant proportion at $p = 0.3$. Such a population configuration appeared to be long term stable (over approximately 20,000 generations) and compared favourably with the value of p resulting from the classical mixed population analysis of the replicator equation, which would proscribe that value of p as $p = V/C$, which in our case would give $p = 0.04/0.05 = 0.8$. However, it is important to point out that, unlike in the replicator equation analysis, the probability values in these simulation results are diverse, with all allowed values represented, and results from an average between two major population contingents that are both far from the average value. In each case the population went into a decline from the grid Dove carrying capacity of approximately 375,000 individuals as mutations took effect and the number of Hawk interactions increases. This can be seen clearly from the plots at times $t = 10,000$. As the simulation progresses, the population divided into two main contingents, (one with $p = 0.3$ and another with $p = 1$ as discussed above), and the spatial dynamics then resembles that in the pure strategy host-parasite case that we examined at the start of this chapter in which the Hawks chase the Dove concentrations across the grid. In the case of the individual payoff structure the population was a little higher, but the proportion of mostly Hawks to mostly Doves was the same for both regimes. Although the probabilities of playing Dove, for both time averaged over the whole simulation and averaged over the population at the final time step were almost exactly the same, the major mostly Hawk contingent in the individual case had a probability of playing Dove of 0.2 whereas in the averaged payoff structure case the main mostly Hawk component had $p = 0.3$. Apart from this difference in the

probability profile and the slightly increased the population level, the change from an averaged to an individual payoff structure had little effect upon the ensuing dynamics.

There are many parameter ranges and initial spatial configurations that could be investigated. For the current case we have briefly explored the effect of holding the value of V constant at 0.04 and varying the value of C. It was observed that for values of C less than V (i.e. for $C \leq 0.04$), the population entered a terminal decline as it mutated towards the Hawk extreme before becoming extinct altogether. It remains for a further extension to determine whether it is a general property of this simulation structure that a stable polymorphism is only in general possible for payoff parameters that satisfy the condition $V \leq C$. It also remains to determine whether the 'granularity' or the size of the allowed mutation in the probability would have any effect on the population dynamics.

6.4 Conclusion

We have investigated an individual based spatial model of the Hawk-Dove game. We have considered both the standard averaged payoff structure, in which the payoff in a Hawk-Hawk contest is $1/2.(V-C)$ for both players, and an individual payoff structure in which there is a winning hawk that receives V and a losing Hawk that receives $-C$. We have considered both random (diffusive random walk) and directed (kairomone sensitive) movement. In common with other investigation of spatial effects in game theory interactions, we have found that there are parameter ranges in which the proportion of Hawks to Doves differs from that predicted by the traditional mean field results of evolutionary game theory. Furthermore, we found long term persistence of coexistence into parameter ranges in which classically we would expect only one or other strategy to survive. Some parameter sensitivity analysis was performed in that

we investigated a range of parameters in which the co existence property obtained. The effect of mutations were considered, of which the most interesting was probably the case of mutation in the strategy followed, for which we had to introduce mixed strategies into the simulation. A surprising finding was that a stable polymorphism resulted with a long term stable population and a long term stable probability of playing Dove.

Chapter 7

Simulation Results for the Rock Scissors Paper Game

This is an example of a three strategy game. The strategies, R, S, P are such that R beats S, S beats P and P beats R. As such the interaction is a non-transitive one and therefore fundamentally different from the two cases considered previously. We consider the form of the game in which there is a small penalty ε for both players in the event of a draw. The payoff matrix we will consider is:

The Rock Scissors Paper game represents the simplest example of a cyclic interaction. Instances from nature of cyclic interactions include the mating strategies of side-blotched lizards [138], overgrowths by sessile marine organisms [139], and in te effect on plant communities of the root hemiparasitic plant Rhinantus minor [147].

A spatial Rock Scissors Paper game was considered in [24], in which spiral waves were reported. This game was considered on a graph in [83], in which it was reported that there is a coexisting equilibrium for all three strategies. A stochastic differential equation approach that considers motility and spatial effects can be found in [112].

The results of our simulations for this game bear the most resemblance to the classical well mixed case and our results are in general accord with what might be expected on the basis of classical results.

$$\begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{pmatrix} -\varepsilon & 0.1 & -0.1 \\ -0.1 & -\varepsilon & 0.1 \\ 0.1 & -0.1 & -\varepsilon \end{pmatrix} \end{array} \tag{7.1}$$

The starting configuration for each simulation is a random spatial distribution of 5,000 agents on a 100 by 100 grid. Each has equal probability of being either an R, S or P player. We consider only pure strategies. These pure strategies are such that one would expect that all three strategies should be present in any potentially stable polymorphic population.

As outlined in Chapter 2, the mixed strategy of $\frac{1}{3}R + \frac{1}{3}S + \frac{1}{3}P$ is an ESS. However, the polymorphic population $\frac{1}{3}R, \frac{1}{3}S, \frac{1}{3}P$ is known to be unstable. This is an example of a discrepancy between the stability criteria in the two cases [6].

7.1 Simulation Results

We consider the effect of kairomone secretion and though we will usually set $\varepsilon = 0.01$, we shall briefly examine the effect of varying this value.

Synchronous Generation

No Kairomone Secretion ($\nu = 0$)

The three populations quickly find a stable level in which roughly equal proportions co-exist. So at any given time approximately one third of the population are Rock players, one third play Scissors and the remaining third play Paper. After half a million time steps (five thousand generations) the mean population levels for R,S,P were 62,893, 62,852 and 63,116 respectively. The fluctuations in these populations were also very similar to one another, with standard deviations for R,S,P of 3,074, 3,257 and 3,229 respectively. There was in fact evident a slight upward trend in the average population values with time. A longer simulation would be required to track this variation.

The grid is populated by a dynamic configuration of the three strategy types.

other work on three strategy competition, see [73]

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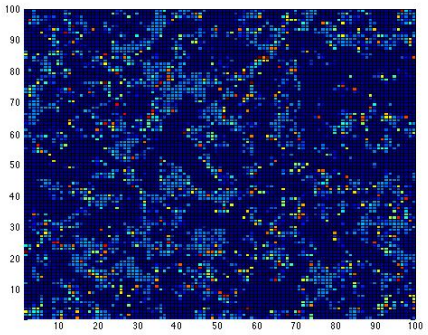	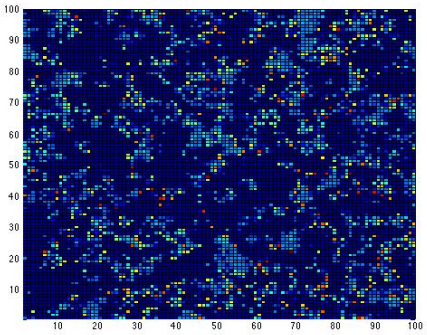
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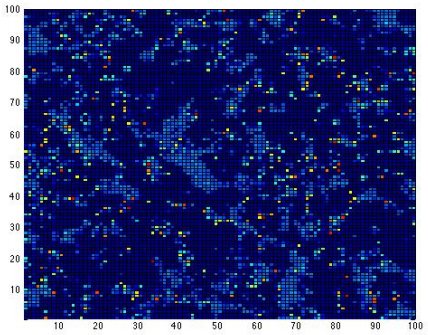	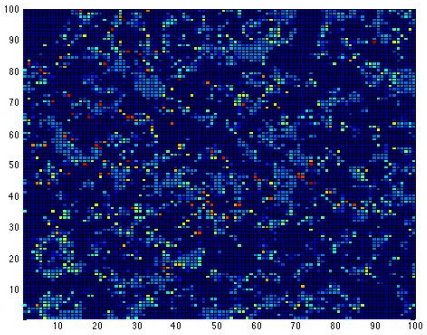
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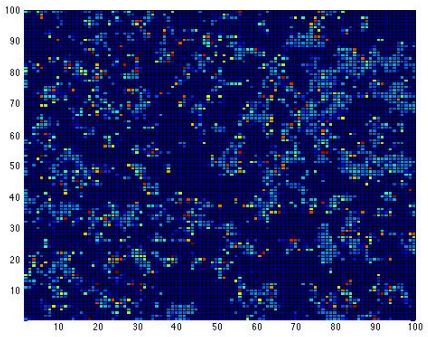
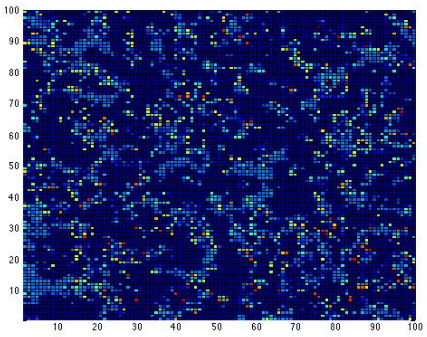
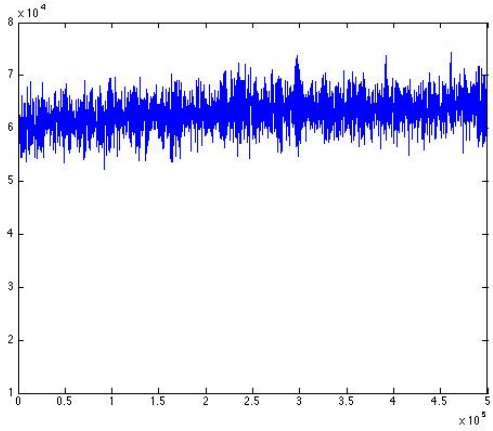
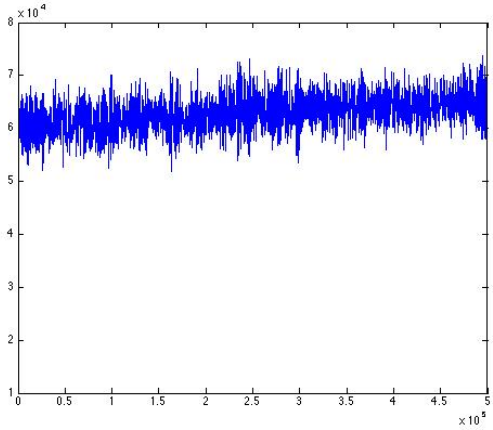
	
Scissors	Scissors

Table 7.1: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is of 5,000 agents each randomly assigned one of the three strategies.

Rock



Scissors



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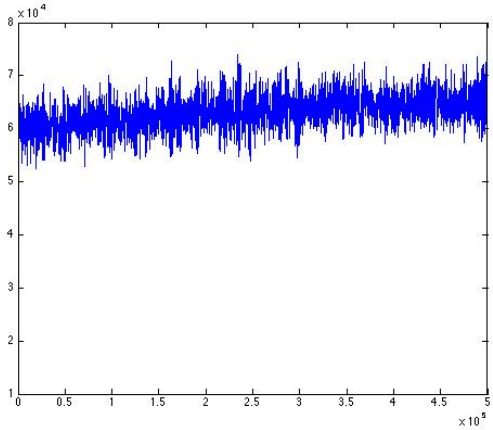

Table 7.2: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of R = 62,893, mean number of S = 62,852 and mean number of P = 63,116. Standard deviations in the populations were 3,074, 3,257 and 3,229 respectively.

With Kairomone Secretion $(\nu = 1)$

The grid is populated by a dynamic configuration of the three strategy types. The secretion of kairomone makes almost no difference to the dynamics, with population levels remaining pretty much as they were in a zero kairomone environment. There is a very minor difference in population levels between the two cases. For example the long term average of R strategists changes from 62,893 to 62,669, representing a decrease of 0.4%. The statistics are similar for the other two strategy types. There is an almost exact one third split between the strategy types (to the second decimal place in percentage terms). Again the standard deviation figures lend support for the view that the population structure is long term stable.

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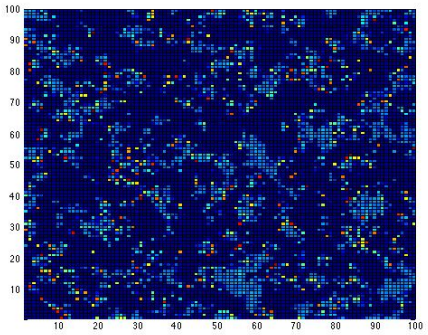
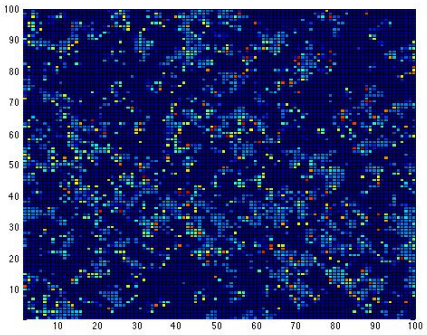
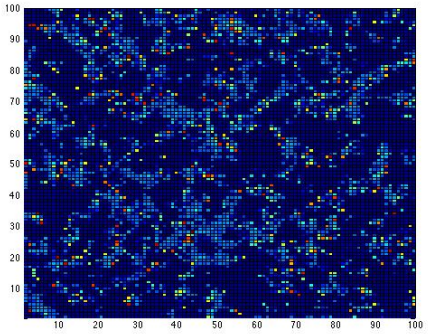
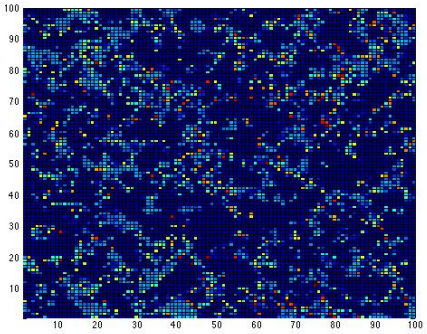
	
Rock	Rock
	
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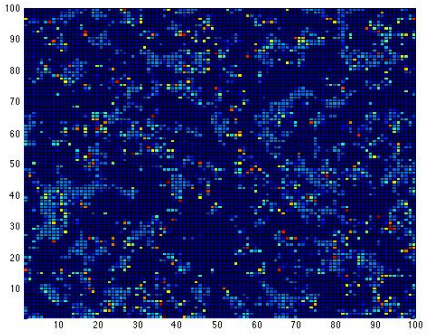
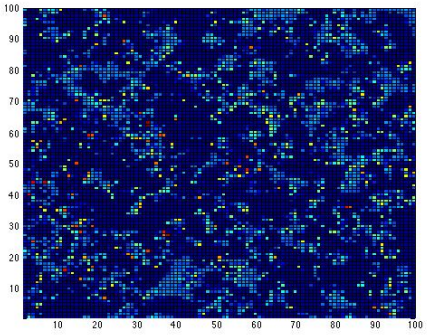
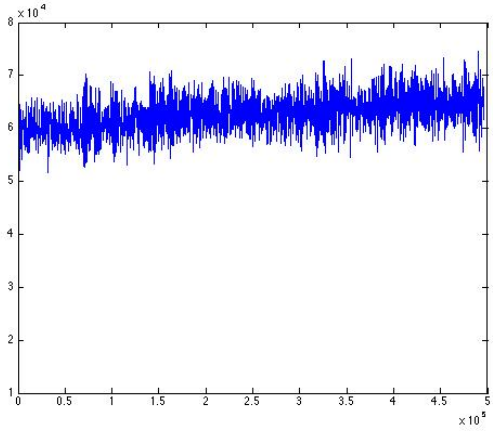
	
Scissors	Scissors

Table 7.3: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is of 5,000 agents each randomly assigned one of the three strategies.

Rock



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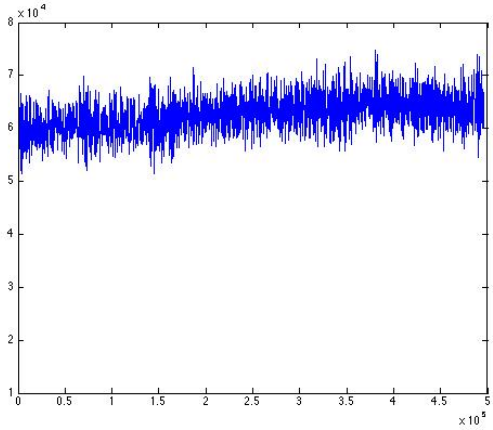

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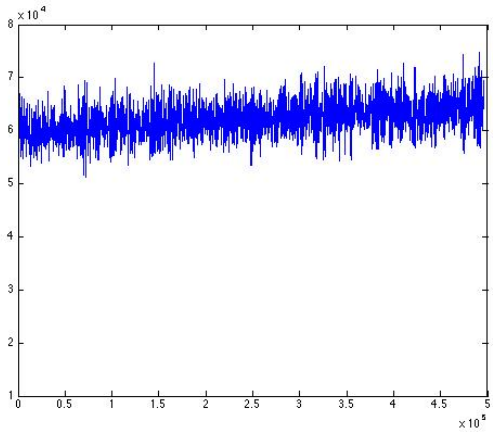

Table 7.4: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of R = 62,669, mean number of S = 62,629 and mean number of P = 62,232. Standard deviations in the populations were 3,205, 3,298 and 3,178 respectively.

Non-Synchronous Generations

No Kairomone $(\nu = 0)$

The spatial distribution of agents is much the same as before, being a dynamically shifting mosaic of local concentrations. Each of the three strategies accounts for very close to 33% of the total population and we have a stable coexisting polymorphism of the three pure strategies. In common with the results from simulations for other games in earlier chapters, allowing non synchronous reproduction has the primary effect of increasing the population size. Compared to the non-synchronous case, the population of R players increases from 62,893 to 86,794, an increase of some 38%. Similar increases occur for the other two strategies. From the standard deviation figures, and from the magnitude of the variations about the mean level, it is clear that none of the populations was in danger of extinction during the course of the five thousand generation simulation.

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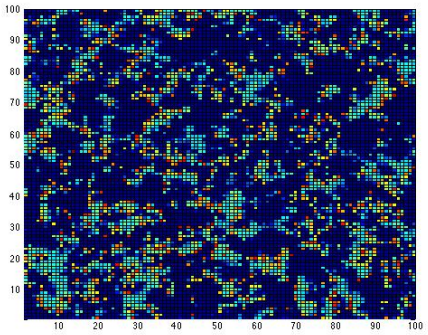	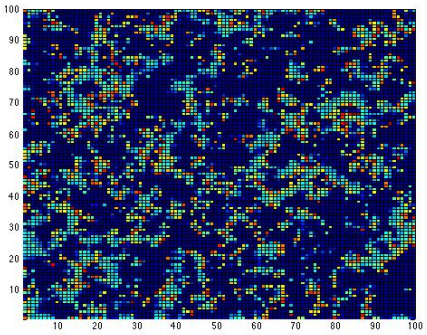
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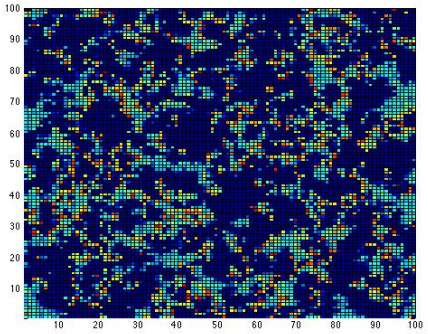	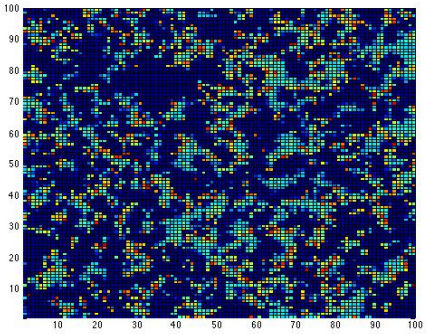
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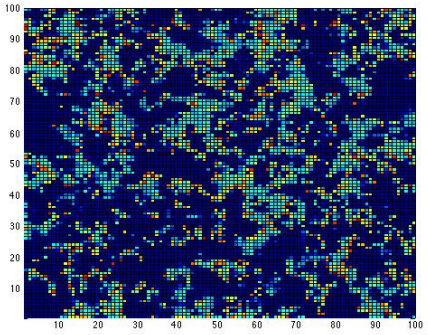
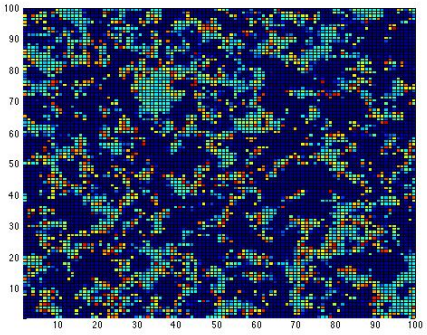
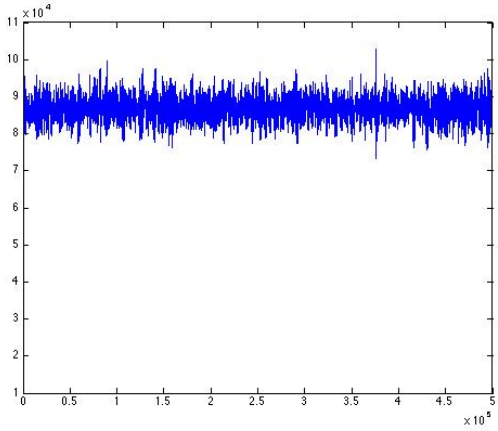
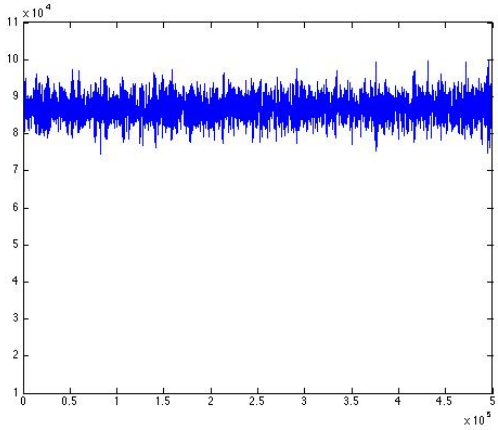
	
Scissors	Scissors

Table 7.5: Snapshots in time depicting spatial distribution of agents. There is no kairomone secretion ($\nu = 0$) and the initial configuration at $t = 0$ is of 5,000 agents each randomly assigned one of the three strategies.

Rock



Scissors



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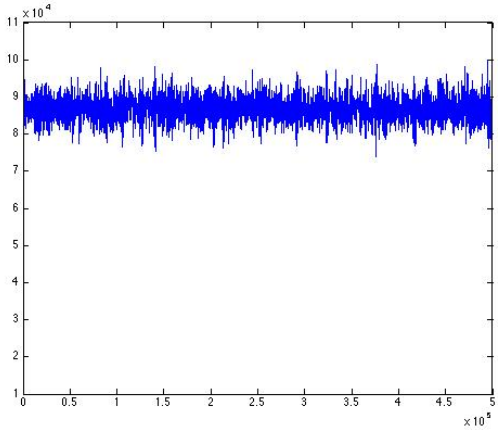

Table 7.6: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of R = 86,794, mean number of S = 86,743 and mean number of P = 86,792. Standard deviations in the populations were 3,458, 3,478 and 3,405 respectively.

With Kairomone $(\nu = 1)$

The spatial distribution is similar to the above simulations. No particular pattern is discernible in the spatial arrangement. Again the long term average distribution approximates the expected one third split to each strategy type. The R players constituted a long term average of 33.345%, S 33.316% and P amounted to 33.339%. This corresponds to approximately 86,500 individuals of each strategy type. The standard deviation in population numbers was an order of magnitude below the population averages at approximately 3,600, indicating that the population structure should remain stable.

Compared to the non-synchronous case, the population of R players increases from 62,669 to 86,475, an increase of some 38%. Similar increases occur for the other two strategies. This situation is very similar to the comparison between the synchronous and non synchronous non kairomone secreting cases. Indeed the populations numbers are almost identical. Thus for this simulation type, the change from synchronous to non-synchronous generation structure seems to have a universally beneficial effect. Whereas the change introduction kairomone secretion seems to have a marginal impact on the dynamics.

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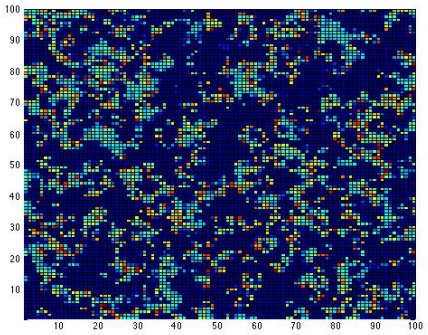	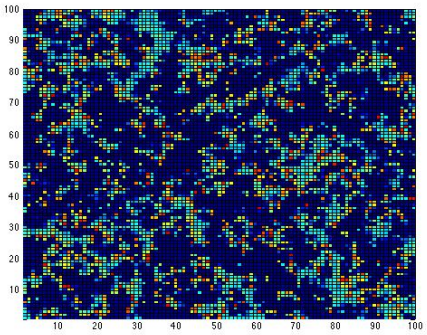
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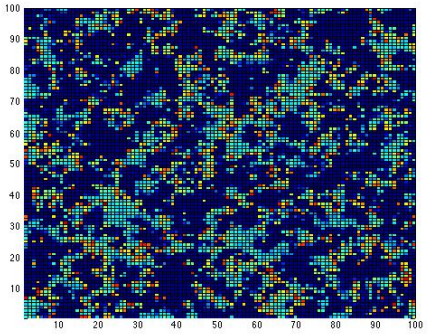	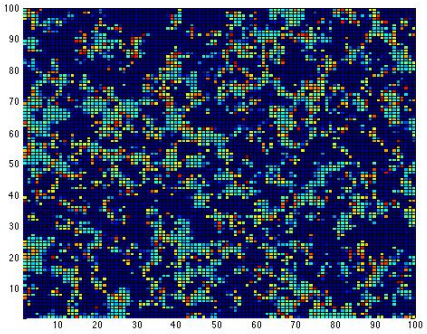
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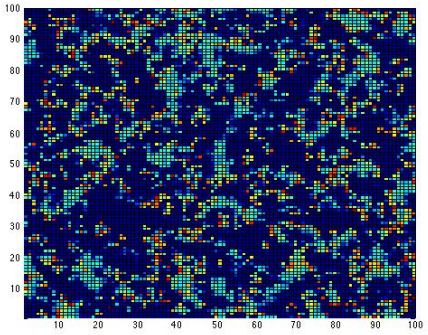
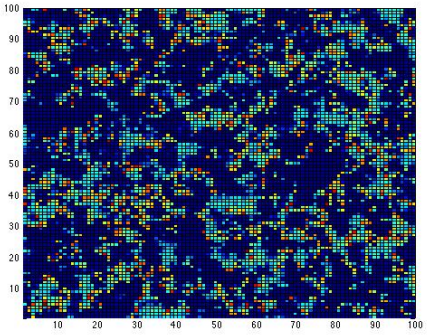
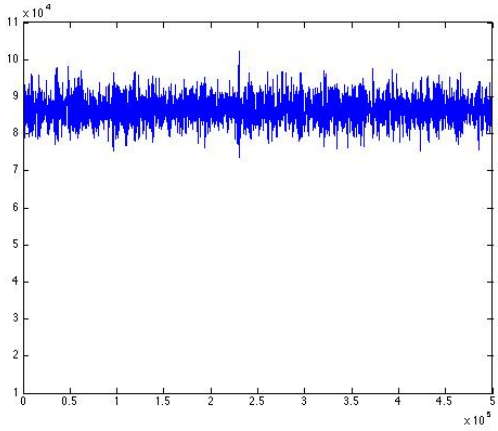
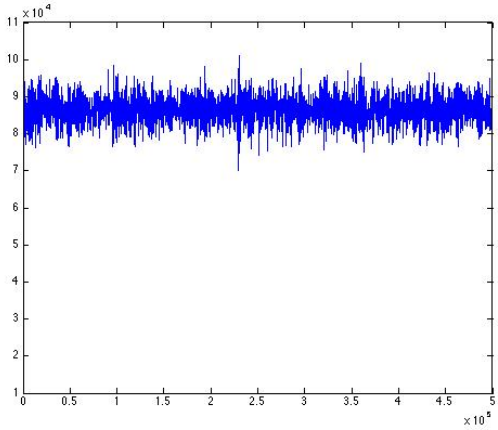
	
Scissors	Scissors

Table 7.7: Snapshots in time depicting spatial distribution of agents. There is kairomone secretion $(\nu = 1)$ and the initial configuration at $t = 0$ is of 5,000 agents each randomly assigned one of the three strategies.

Rock



Scissors



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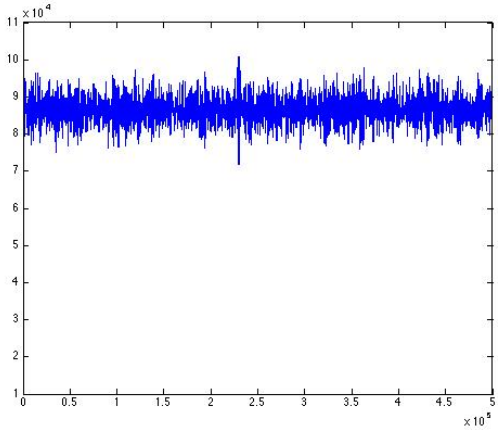

Table 7.8: Plots of the agent population in time. The populations exhibit long term stable co-existence, each fluctuating about a stable long term average. Mean number of R = 86,457, mean number of S = 86,399 and mean number of P = 86,459. Standard deviations in the populations were 3,565, 3,587 and 3,574 respectively.

Discussion

The primary result of these simulations is that we observe a long term stable coexistence of the three pure strategies. There is an almost exact one third split in population between the three different strategy types. There results no apparent pattern to the distribution of agents on the grid, though the distribution is dynamic and constantly chaging. Kairomone secretion seems to have virtually no effect on the dynamics, with population levels virtually unchanged. Changing from a synchronous to a non-synchronous generation structure results in a general increase in the population of about 38%. The total population increasing from approximately 188,000 to 260,00 individuals. These results are outlined in the table below.

Table 7.9: Comparison of Simulation Results for Case $\varepsilon = 0.01$

Case	Generation Structure	Kairomone (v)	R Mean	S Mean	P Mean	Comment
1	Synchronous	0	62,893	62,852	63,116	Coexistence
2	Synchronous	1	62,669	62,629	62,232	Coexistence
1	Non-Synchronous	0	86,794	86,743	86,792	Coexistence
2	Non-Synchronous	1	86,475	86,399	86,459	Coexistence

The Effect of Changing ε

The dynamics are very sensitive to the value of ε. A slight reduction in ε to 0.007 or below leads to the eventual mutual extinction of all three populations. Reducing its value slightly to 0.008 leads to equilibrium mean levels of approximately one half what they were for $\varepsilon = 0.1$, at some 32,000 individuals. Thus the classic Rock Paper Scissors game in which $\varepsilon = 0$ does not in our case lead to a stable coexisting polymorphic population.

Reducing the value of ε by a factor of 10 to 0.001 results in extinction of the entire population. Thus in this parameter range, a significant value of ε is required to stabilise the populations.

As an example we give data for the effect of varying V for simulations in synchronous generation, zero kairomone case. There is a clear trend for the population to increase with increasing $|epsilon$.

Table 7.10: Comparison of Simulation Results for Different Values of ε

V	R Mean	S Mean	P Mean
0.07	0	0	0
0.008	34799	35265	35485
0.009	48338	48333	48158
0.01	62893	62852	63116
0.011	70643	70697	70948
0.012	74910	75386	76178

Variation of Population with Value of ε

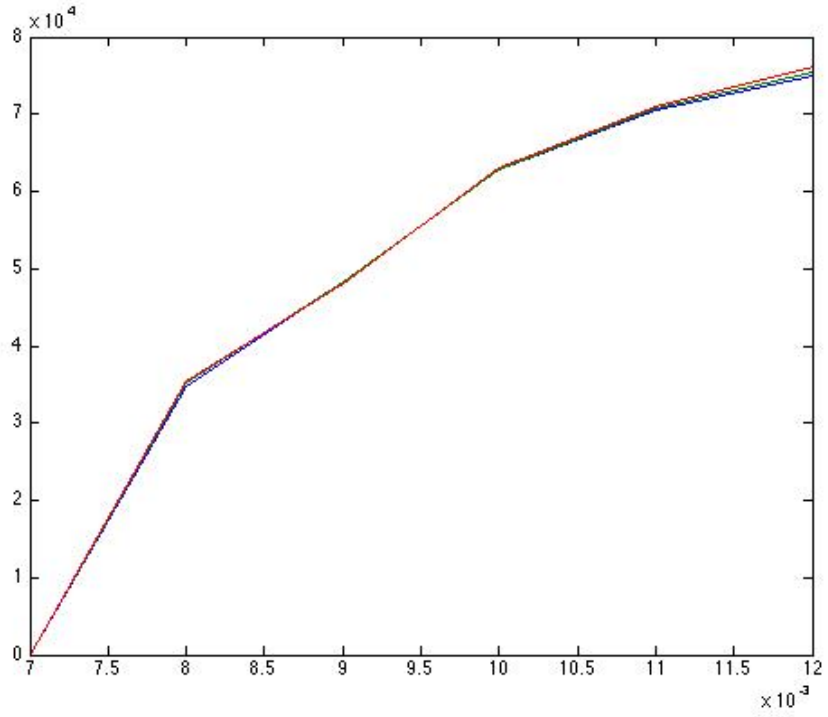

Table 7.11: The population of all three agent types are here plotted by separate lines, but they are difficult to distinguish as the population numbers are so similar. There is a monotonic increase in population with the value of ε.

7.2 Conclusion

In this game mutual coexistence is necessary for stability due to the cyclic nature of the interaction. Strategists of the R variety gain positive payoff from interactions with S, which in turn gain from the P players, which in turn gain from the R players. Should any one component of this triad be removed from the population, the other two will not be able to survive. The population attains its own equilibrium level with an overall percentage distribution of almost exactly one third per strategy type. This reflects what is known to be the stable state in the classical replicator analysis. The spatial distribution is however far from even, with a fluctuating network of voids and population centres. Where one strategy concentration is suffering from an interaction with another in one locality, the same strategy will be winning against another at a different location. Globally, over the whole grid, these fluctuations average out and all three populations exhibit a limited fluctuation about a seemingly well defined long term average value.

Chapter 8

Conclusions

In this thesis we have attempted to consider a form of game theory scenario in a spatial setting. Some of the results presented seem to be contrary to what would be expected on the basis of the standard ESS or replicator analysis or indeed differ from the Nash Equilibrium itself. The implications for the applicability of game theory to spatial environments is not certain. We have found simulations of the Prisoners' Dilemma in which Always Cooperate and Always Defect are able to coexist in an indefinite and stable equilibrium. Here the Nash equilibrium would clearly be to defect. Yet when agents are allowed to 'choose' a strategy by the mechanism of mutation, the population does indeed move steadily towards the Nash equilibrium and thereby also to extinction. We have also encountered Hawk-Dove simulations (cases for $V > C$) in which for example the ESS of playing Hawk is however incapable of replacing an existing Dove population. We have also seen simulations (cases in which $V < C$) in which the proportions of Hawks and Doves in the population does not accord with that expected on the basis of the non spatial analysis (which is for proportion V/C to play Hawk).

For the Hawk-Dove game coexistence of strategists was pure strategists was typically

observed for payoff matrix parameters that were intermediate between stable populations of all Doves and all Hawks. And some of the most interesting behaviour in terms of spatial patterns arose from cases from the edge of this parameter range in which coexistence was more unstable. Often the most interesting phenomena, such as the spiral wave type patterns, are observed in a regime where both populations have become very close to extinction.

In the case of the Prisoners' Dilemma, Mutual coexistence obtains in a payoff parameter range in which the AD represent a mild to severe parasitism on the ambient AC population. To borrow the language of diseases, for 'infections' that are too mild, corresponding to low values of the Defect-Defect payoff T, the AD population fails to establish itself as a permanent feature of the population. For large values of T, or a highly virulent infection, the AD are again unable to establish themselves as a long term component of the population. This is because they act to so severely deplete their host population that the AC host numbers enter a terminal decline that thereby affects the AD in that insufficient hosts are available to allow a sustainable AD population. Typically in such parameter ranges, the result is either the extinction of the AD after an initial devastation of AC as a wave of AD expands to the edges of the grid, or else mutual extinction of both strategy types. For intermediate values of T, perhaps representing a moderate infection strength, long term coexistence is sometime possible. In these populations the AC numbers are regulated to a stable but lower level than in the case without infection. The situation resembles an endemic infection, with patches of AC without AD in recovery and expanding, and other patches of AC in terminal decline as they encounter local concentrations of AD.

We have also considered the effects of allowing kairomone secretion. The results were somewhat mixed depending on the game being considered, though kairomone secretion definitely had some effect. We have further gone on to consider the effects of allowing kairomone productivity to change with each generation by mutation. Time

so far has only allowed a small number of such simulations, but preliminary results suggest a pressure in the cases examined towards increased kairomone secretion.

Simulations were conducted using both synchronous and non-synchronous generation structures. These changes had some effect on the dynamics, and in the Hawk-Dove game in particular they had a notable effect on the parameter range over which coexistence could be observed. Nonetheless, despite this change the general character of the simulation results remains unchanged, which is to say that parameter values for payoff matrix elements can be found that permit coexistence in a spatial setting.

In the simulation setup the absolute size of the payoff makes a crucial difference to the outcome. For example, in a Hawk-Dove game interaction, if the payoff for Hawk against Hawk is so small that the payoff typically accumulated in an agents lifetime is insufficient for it to be able to leave behind offspring, then a population of pure Hawks will not be able to survive. In this situation Hawks can be compelled to become parasitic upon Doves as this may be the only interaction by which sufficient payoff for reproduction may be accumulated. Similar remarks apply to the Prisoners' Dilemma simulations, in which the payoff for mutual defection is kept so low that the AD cannot gather sufficient accumulated payoff to give rise to viable numbers of offspring unless there are AC present with whom they can interact. So the absolute size of payoff parameters in relation to the agent lifetime is an important factor consider. The ratio of the different payoffs is also important. For example, for very large values of V in the Hawk-Dove game, or T in the Prisoners' Dilemma, coexistence may not be possible and depending on the other payoff parameters the result would either be extinction of the aggressive strategy due to overgrazing, or else if the aggressive mutual interactions are fruitful enough, they will come to take over the entire population.

The effect of allowing the strategies themselves to mutate was explored. In the limited investigation currently available, it was found that an Always Cooperating population

in the Prisoner's dilemma would gradually but consistently mutate into an Always Defect population, and thence become extinct. The situation was a little more interesting in the case of the Hawk-Dove game in that an initial population of Doves evolved into a stable polymorphism in which there were significant numbers of pure Doves alongside a significant and stable contingent of players that played Hawk most of the time. Possible conditions on when such behaviour may be stable remain to be explored.

The moral of the story concerning game theory interactions seems to be that one needs to be precise regarding the set up and interaction before outcomes can be predicted. The classical infinite well mixed population results do not necessarily hold once spatial effects are included and may not be a reliable guide in general. The Nash equilibrium is by no means observed to the a universally favoured or stable state for a population of spatial strategists, just as it also is not often the favoured choice of experimental subjects placed in game theory scenarios.

quoting [104]: " ...it does not seem plausible to expect general laws that could be applied in a wide range of practical settings. On the contrary, a close modelling including the kind of game, the evolutionary dynamics and the population structure of the concrete problem seems mandatory to reach sound and compelling conclusions." It was ever thus...

Quotation

"*Annoying! The same old story! When one has finished one's house one realizes that while doing so one has learnt unawares something one abolutely had to know before one began to build. The everlasting pitiful 'too late!'-The melancholy of everything finished!*"

Friedrich Nietzsche, *Beyond Good and Evil*.

Bibliography

[1] Von Neuman, J. & Morgenstern, O. [1953], *Theory of Games and Economic Behaviour*, Princeton University Press.

[2] Poundstone, J. [1992], *The Prisoners' Dilemma*, Doubleday.

[3] Darwin, C. [2004], *The Descent of Man*, Penguin Classics.

[4] Hobbes, T. [2004], *Leviathan*, Penguin Classics.

[5] Wilson, E. O. [2012], *The Social Conquest of Earth*, W. W. Norton & Co..

[6] Maynard Smith, J. [1982], *Evolution and the Theory of Games*, Cambridge University Press.

[7] Skryms, B. [1996], *Evolution of the Social Contract*, Cambridge University Press.

[8] Gibbons, R. [1992], *A Primer in Game Theory*, Harvester Wheatsheaf.

[9] Webb, J. [2007], *Game Theory: Decisions, Interactions and Evolution*, Springer.

[10] Schelling, T. [1980], *The Strategy of Conflict*, Harvard University Press.

[11] Trivers, R. L. [1971]. The Evolution of Reciprocal Altruism. *Q. Rev. Biol.* **46**, 35–57.

[12] Maynard Smith, J. [1964]. Group Selection and Kin Selection. *Nature.* **201**, 1145–1147.

[13] Skryms, B. [2004], *The Stag Hunt and the Evolution of Social Structure*, Cambridge University Press.

[14] Maynard Smith, J. & Price, G.R. [1973]. The Logic of Animal Conflict. *Nature* **273**, 15–18.

[15] Taylor, P.D. & Jonker, L.B. [1978]. Evolutionary Stable Strategies and Game Dynamics *Mathematical Biosciences* **40**, 145–156.

[16] Zeeman, E.C. [1980]. Population Dynamics from Game Theory *Global Theory of Dynamical Systems* Spinger-Verlag

[17] Hofbauer, J & Sigmund, K [1998]. *Evolutionary Games and Population Dynamics*, Cambridge University Press.

[18] Axelrod, R [1984]. *The Evolution of Cooperation*, Basic Books.

[19] Axelrod, R. & Hamilton, W.D. [1981]. The Evolution of Cooperation. *Science* **211**, 1390–1396.

[20] Axelrod, R [1997]. *The Complexity of Cooperation*, Princeton University Press.

[21] Nowak, M.A. & May, R.M. [1993]. The Spatial Dilemmas of Evolution. *Int. Journal of Bifurcations and Chaos* **3**, 35.

[22] Nowak, M.A. & May, R.M. [1992]. Evolutionary Games and Spatial Chaos. *Nature* **359**, 826–829.

[23] Nowak, M.A. & Bonhoeffer, S. & May, R.M. [1994]. Spatial Games and the Maintenance of Cooperation. *PNAS* **91**, 4877–4881.

[24] Nowak, M.A. & Bonhoeffer, S. & May, R.M. [1994]. More Spatial Games. *Int. Journal of Bifurcations and Chaos* **4**, 33–56.

[25] Schofield, P. & Chaplain, M.A.J. & Hubbard, S. [2002]. Mathematical Modelling of Host-Parasitiod Systems: Effects of Chemically Mediated Parasitoid Foraging Strategies on Within- and Between-generation Spatio-temporal Dynamics. *J. Math. Biol.* **214**, 31–47.

[26] Schofield, P. & Chaplain, M.A.J. & Hubbard, S. [2005]. Dynamic Heterogeneous Spatio-Temporal Pattern Formation in Host-Parasitiod Systems with Synchronised Generations. *J. Math. Biol.* **50**, 559–583.

[27] Schofield, P. & Chaplain, M.A.J. & Hubbard, S. [2005]. Evolution of Searching and Life History Characteristics in Individual Based Models of Host-Parasitoid-Microbe Associations. *J. Theor. Biol.* **237**, 1–16.

[28] Anderson, A.R.A. & Chaplain, M.A.J. [1998]. Mathematical Models of Tumour-induced Angiogenisis. *Bull. Math. Biol* **60**, 857–899.

[29] Nowak, M.A. [2006]. *Evolutionary Dynamics*, Belknap/Harvard.

[30] Huberman, B.A. & Glance, N. S. [1993]. Evolutionary Games and Computer Simulations. *PNAS* **90**, 7716–7718.

[31] Killingback, T. & Doebrli, M. [1996]. Spatial Evolutionary Game Theory: Hawks and Doves Revisited. *Proceedings: Biological Sciences* **263, No. 1374**, 1135–1144.

[32] Reichenbach, T. & Mobilia, M. & Frey, E. [2007]. Mobility Promotes and Jeopardizes Biodiversity in Rock-Paper-Scissors Games. *Nature* **448**, 1046–1049.

[33] Durrett, R. & Levin, S. [1993]. The Importance of Being Discrete (and Spatial). *Thoer. Popul. Biol.* **46**, 363–394.

[34] Bach, L.A. & Sumpter, D.J.T. & Alsner, J. & Loeschcke, V. [2003]. Spatial Evolutionary Games of Interaction among Generic Cancer Cells. *Journal of Theoretical Medicine* **5**, 47–58.

[35] Kirchkamp, O. [2000]. Spatial Evolution of Automata in the Prisoners' Dilemma. *Journal of Economic Behaviour and organization* **43**, 239–262.

[36] Levin, S. [1974]. Dispersion and Population Interactions. *The American Naturalist* **108**, 207–228.

[37] Anderson, A [1996], The Role of Structure in Mediating Chemical Gradients and Nematode Movement: Theory and simulation *PhD. thesis, University of Dundee*

[38] Anderson, A. & Chaplain, M. [1998], Continuous and Discrete Mathematical Models Tumour-Induced Angiogenisis. *Bull. Math. Biol.,* **60***, 857-899*

[39] Okubo, A. & Levin, S. [2001]. *Diffusion and Ecological Problems*, Springer.

[40] Bowles, S. & Gintis, H. [2011]. *A Cooperative Species*, Princeton University Press.

[41] Sigmund, K. [1993]. *Games of Life*, Oxford University Press.

[42] Hassell, M. P. [2000]. *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*, Oxford University Press.

[43] Ed. Katz, L. D. [2002]. *Evolutionary Origins of Morality*, Imprint Academic.

[44] Britton, N. F. [2003]. *Essential Mathematical Biology*, Springer.

[45] Murray, J. D. [1980]. *Mathematical Biology*, Springer-Verlag.

[46] May, R. [2001]. *Stability and Complexity in Model Ecosystems*, Princeton University Press.

[47] Edelstein-Keshet, L. [2005]. *Mathematical Models in Biology*, SIAM.

[48] Fehr, E. & Fischbacher, U. [2003]. The Nature of Human Altruism. *Nature* **425**, 785–791.

[49] Oosterbeek, H. & Sloof, R. & Van de Kuilen, G [2003]. Cultural Differences in Ultimatum Game Experiments: Evidence from a Meta-Analysis. *Experimental Economics* **7**, 171–188.

[50] Hofbauer, J. & Sigmund, K. [2003]. Evolutionary Game Dynamics *Bulletin of the American Mathematical Society* **40**, 479–519.

[51] Durrett, R. [1999]. Stochastic Spatial Models *SIAM Rev.* **41**, 677–718.

[52] Durrett, R. & Levin, S. [1994].Stochastic Spatial Models: A User's Guide to Ecological Applications *Phil. Trans. B* **343**, 329–350.

[53] Hofbauer, J. & Sigmund, K. [1993]. The Spatial Dilemmas of Evolution*International Journal of Bifurcation and Chaos* **3**, 35–78.

[54] Keeling, M. J. [2000]. Evolutionary Dynamics in Spatial Host-Parasite Systems *The Geometry of Ecological Interactions* Cambridge University Press.

[55] Gintis, H. [2009]. *The Bounds of Reason: Game Theory and the Unification of the Behavioural Sciences*, Princeton University Press.

[56] Riolo, R. & Cohen, M. D. & Axelrod, R [2009]. *Evolution of Cooperation Without Reciprocity*, *Nature* **414**, 441–443.

[57] Levin, S. & Grenfell, B. & Hastings, A. & Perelson, A [1997]. *Mathematical and Computational Challenges in Population Biology and Ecosystems Science*, *Science* **275**, 334–343.

[58] Santos, F. C. & Rodrigues, J. F. & Pacheco, J. M. [2006]. *Graph Topology Plays a Determinate Role in the Evolution of Cooperation*, *Proc. R. Soc. B* **273**, 51–55.

[59] Santos, F. C. & Pacheco, J. M. [2006]. *A New Route to the Evolution of Cooperation*, *Europ. Soc. Evolu. Biol.* **19**, 726–733.

[60] Sato, K. & Matsuda, H. & Akira, S. [1994]Pathogen Invasion and Host Extinction in Lattice Structured Populations *J. Math. Biol* **32**, 251–268.

[61] Ludwig, D. & Aronson, D. G. & Weinberger, H. F. [1979]. Spatial Patterning of the Spruce Budworm *J. Math. Biol* **8**, 217–258.

[62] Yachi, S. & Kawasaki, K. & Shigesada, N. & Teramoto, E. [1989]. Spatial Patterns of Propagating Waves of Fox Rabies *Forma* **4**, 3–12.

[63] May, R. M. & Anderson, R. M. [1979]. Population Biology of Infectious Diseases: Pat II *Nature* **280**, 455–461.

[64] May, R. M. & Anderson, R. M. [1983]. Epidemiology and Genetics in the Coevolution of Parasites and Hosts *Proc. R. Soc. Lond., Ser. B* **219**, 281–313.

[65] May, R. M. & Anderson, R. M. [1987]. Transmission Dynamics of HIV Infection *Nature* **326**, 137–142.

[66] May, R. M. & Anderson, R. M. [1992]. Infectious Diseases of Humans, Oxford University Press

[67] Levin, S. A. [1974]. Dispersion and Population Interactions *Am. Nat.* **108**, 207–228.

[68] Mimura, M. [1983]. Some Reaction-Diffusion Equations Arising in Population Dynamics *Contemp. Math.* **17**, 343–351.

[69] Cantrell, R. S. & Cosner, C. [1991]. The Effects of Spatial Heterogeniety in Population Dynamics *J. Math. Biol.* **29**, 315–338.

[70] Levins, R. [1969]. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control *Bull. Entomol. Soc. Am.* **15**, 237–240.

[71] Chesson, P. L. [1985]. Coexistence of Competitors in Spatially and Temporally Varying Environments. A look at the Combined Effects of Different Sorts of Variability *Theor. Popul. Biol.* **28**, 263–287.

[72] Hanski, I. A. & Gilpin, M. E. [1996]. Metapopulation Biology: Ecology, Genetics and Evolution *Academic Press, New Yourk*

[73] Durrett, R. & Levin, S. [1998]. Spatial Aspects of Interspecific Competition *Theor. Popul. Biol.* **53**, 30–43.

[74] Rand, D. A. & Keeling, M. & Wilson, H. B. [1995]. Invasion, Stability and Evolution to Criticality in Spatially Extended, Artificial Host-Pathogen Ecologies *Proc. R. Soc. Lond. B* **259**, 55–63.

[75] Comins, H. N. & Hassell, M. P. & May, R. M. [1992]. The Spatial Dynamics of Host Parasitoid Systems *J. Anim. Ecol.* **61**, 735–748.

[76] Grenfell, B. & Harwood, J. [1997]. (Meta)population Dynamics of Infectious Diseases *Trends Ecol. Evol.* **12**, 395–399.

[77] Wallinger, J. & Edmunds, W. J. &Kretzschmar, M. [1999]. Perpective: Human Contact Patterns and the Spread of Airborne Infectious Disease *Trends Microbiol.* **7**, 372–377.

[78] Tilman, D. & Karevia, P. [1996]. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interaction*, Princeton University Press.

[79] Mollison, S. [1977]. Spatial Contact Models for Ecological and Epidemic Spread *J. R. Statist. Soc. B* **39**, 283–326.

[80] Levin, S. & Durrett, R. [1996]. From Individuals to Epidemics *Proc. R. Soc. Lond. B.* **351**, 1615–1621.

[81] Read, J. M. & Keeling, M. [2003]. Disease Evolution on Networks: the Role of Contact Structure*Proc. R. Soc. Lond. B* **270**, 699–708.

[82] Greig, D.. & Travisano, M. [2004]. *The Prisoner's Dilemma and Polymorphism in Yeast SUC Genes*, *Proc. R. Soc. Lond. B* **271**, S25–S26.

[83] Ohtsuki, H. & Nowak, M. A. [2006]. *The Replicator Equation on Graphs*, *J. Theor. Biol.* **243**, 86–97.

[84] Killingback, T. & Doebeli, M. [1996]. *Spatial Evolutionary Game Theory: Hawks and Doves*, *Proc. R. Soc. B* **263**, 1135–1144.

[85] Ifti, M. & Killingback, T. & Doebeli, M [2004]. *Effects of Neighbourhood Size and Connectivity on the Spatial Continuous Prisoner's Dilemma*, *J. Theor. Biol.* **231**, 97–106.

[86] Vainstein, M. H. & Silva, A. T. C. & Arenzon, J. J. [2007]. *Does Mobility Decrease Cooperation*, *J. Theor. Biol.* **244**, 722–728.

[87] Ohtsuki, H.. & Nowak, M. A. [2006]. *Evolutionary Games on Cycles*, *Proc. R. Soc. B* **273**, 2249–2256.

[88] Aktipis, A. [2004]. *Know When to Walk Away: Contingent Movement and the Evolution of Cooperation*, *J. Theor. Biol.* **231**, 249–260.

[89] Haraguchi, Y. & Sasaki A. [2000]. *The Evolution of Parasite Virulence and Transmission in a Spatially Structured Population*, *J. Theor. Biol.* **203**, 85–96.

[90] Nowak, M. A. & Tarnita, C. E. & Antal. T. [2010]. *TEvolutionary Dynamics in Structured Popualtions*, *Phil. Trans. R. Soc. B* **365**, 19–30.

[91] Tomasini, M. & Luthie, L. & Giacobini, M [2006]. *Hawks and Doves on Small-World Networks*, *Phys. Rev. E.* **73**, 86–97.

[92] Szolnoki, A. & Perc, M. & Danku, Z. [2008]. *Making New Connections Towards Cooperation in the Prisoner's Dilemma Game*, *EPL.* **84**, No. 5.

[93] Brauchli, K. & Killingback, T. & Doebeli, M. [1999]. *TEvolution of Cooperation in Spatially Structured Populations*, *J. Theor. Biol.* **200**, 405–417.

[94] Hauert, C. [2002]. *Effects of Space in 2 X 2 Games*, *Int. J. of Bif. and Chaos* **12**, 1531–1548.

[95] Hauert, C. [2001]. *Fundamental Clusters in Spatial 2 X 2 Games*, *Proc. Biol. Sci.* **268**, 761–769.

[96] Schweitzer, F. & Behera, L. & Muhlenbein. H [2002]. *Evolution of Cooperation in a Spatial Prisoner's Dilemma*, *Advan. Compl. Sys* . **5**, 269–299.

[97] Vulic, M. & Kolter, R. [2001]. *Evolutionary Cheating in Escherichia coli Stationary Phase Cultures*, *Genetics* **158**, 519–526.

[98] Lieberman, E. & Hauert, C. & Nowak, M. A. [2006]. *Evolutionary Dynamics on Graphs*, *Nature* **433**, 312–316.

[99] Dawkins, R. [1982]. *The Extended Phenotype*. Freeman, Oxford.

[100] Lion, S..& Baalen, M. B. [2008]. *Self-Structuring in Spatial Evolutionary Ecology*, *Ecology Letters* **11**, 277–295.

[101] Kerr, B. & Neuhauser, C. & Bohannan, B. J. M. & Dean, A. M. [2006]. *Local Migration Promotes Competitive Restraint in a Host-Pathogen 'Tragedy of the Commons'*, *Nature* **442**, 75–78.

[102] Kerr, B. & Riley, M. A. & Feldman, M. W. & Bohannan, B. J. M. [2002]. Local Dispersal Promotes Biodiversity in a Real-Life Game of Rock-Paper-Scissors, *Nature* **418**, 171–174.

[103] Boots, M. & Mealor, M. [2007]. Local Interactions Select for Lower Pathogen Infectivity, *Science.* **315**, 1284–1286.

[104] Roca, C. P. & Cuesta, J. A. & Sanchez, A. [2009]. Effect of Spatial Structure on the Evolution of Cooperation, *Phys. Rev. E* **80**

[105] Poncela, J. & Gomez-Gardenes, J. & Traulsen, A. & Moreno, M. [2009]. Evolutionary Game Dynamic in a Growing Structured Population, *New J. Phys.* **11**, 1284–1286.

[106] Taylor, C. & Nowak, M. A. [2007]. Transforming the Dilemma, *Evolution* **61**, 2281–2292.

[107] O'Keefe, K. J. & Antonovics, J. [2002]. Playing by Different Rules: The Evolution of Virulence in Sterilizing Pathogens, *Am. Naturalist* **159**, 597–605.

[108] Pacheco, J. M. & Traulsen, A. & Ohtsuki, H. & Nowak, M. A. [2007]. Repeated Games and Direct Reciprocity Under Active Linking, *J. Theor. Biol.* **250**, 723–731.

[109] Szolnoki, A. & Perc, M. [2009]. Emergence of Multilevel Selection in the Prisoner's Dilemma Game on Coevolving Random Networks, *New J. of Phys.* **11**.

[110] Allen, B. & Traulsen, A. & Tarnita, C., & Nowak, M. A. [2007]. How Mutation Affects Evolutionary Games on Graphs, *J. Theor. Biol.* **299**, 97–105.

[111] Nowak, M. A. & Sigmund, K. [2000]. *Games on Grids*, in *The Geometry of Ecological Interactions*, Cambridge University Press.

[112] Reichenbch, T. & Mobilia, M. & Frey, E. [2008]. Self-Organization of Mobile Populations in Cyclic Competition, *J. Theor. Biol.*. **254**, 368–383

[113] Tomasini, M. & Luthie, L. & Pestelacci, E. [2007]. *Social Dilemmas and Cooperation in Complex Networks*, *Int. J. Mod. Phys. C.* **18**, 1173.

[114] Yamamura, N. & Higashi, M. & Behera, N. & Wakano, J. Y. [2003]. Evolution of Mutalism Through Spatial Effects, *J. Theor. Biol.* **226**, 421–428.

[115] Thompson, J. N. [2005]. *The Geographic Mosaic of Coevolution*, University of Chicago Press.

[116] Nowak, M. A. & Ohtsuki, H. [2008]. Evolutionary Stability on Graphs *J. Theor. Biol.* **251**, 698–707.

[117] Duran, O. & Mulet, R. [2005]. Evolutionary Prisoner's Dilemma in Random Graphs *Physica D: Nonlinear Phenomena.* **208**, 257–265.

[118] Szolnoki, A. & Perc, M. [2009]. Promoting Cooperation in Social Dilemmas via Simple Coevolutionary Rules *European. Phys. J. B* **67**, 337–344.

[119] Szabo, G. & Szolnoki, A. & Vukov, J. [2009]. Selection of Dynamical Rules in Spatial Prisoner's Dilemma Games. *E. P. L.* **87**

[120] Sicardi, E. A. & Fort, H. & Vainstein, M. H. & Arenzon, J. J. [2009]. Random Mobility and Spatial Structure Often Enhance Cooperation, *J. Theor. Biol.* **256**, 240–246.

[121] Dugatkin, L. A. & Wilson, D. S. [1991]. Rover- a Strategy for Exploiting Cooperators in a Patchy Environment, *American Naturalist* **138**, 687–701.

[122] Hamilton, I. M. & Taborsky, M. [2005]. Contingent Movement and Cooperation Evolve Under Generalized Reciprocity, *Proc. R. Soc. B* **268**, 761–769.

[123] Koella, J. C. [2000]. The Spatial spread of Altruism Versus the Evolutionary Response of Egoists, *Proc. R. Soc. B* **267**, 1979–1985.

[124] Le Galliard, J. F. & Ferriere, J-F. & Dieckmann, U. [2005]. Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility, *Am. Nat.* **165**, 206–224.

[125] Van Baalen, M. & Rand, D. A. [1998]. The Unit of Selection in Viscous Populations and the Evolution of Altruism, *J. Theor. Biol.* **193**, 631–648.

[126] Kobayashi, H. & Kohshima, S. [2001]. Unique Morphology of the Human eye and its Adaptive meaning: Comparative Studdies on external Morphology of the Primate Eye , *J. Human Evolution.* **40**, 419–435.

[127] Baron-Cohen, S. [1994]. How to Build a Baby that Can Read Minds: Cognitive Mechanisms in Mindreading, *Current Psychology of Cognition.* **13**, 513–552.

[128] Perrett, D. I. & Emery, N. J. [1994]. Understanding the Intentions of Others from Visual Signals: Neurophysiological Evidence, *Current Psychology of Cognition* **13**, 683–694.

[129] Jellema, T. & baker, C. I. & Wicker, B. & Perrett, D. I. [2000]. Neural Representation for the Perception of the Intentionality of Hand Actions, *Brain and Cognition* **44**, 280–302.

[130] Perrett, D. I. [2010]. *In Your Face*. Palgrave Macmillan.

[131] Ferriere, R. & Michod, R. [1995]. Invading Wave of Cooperation in a Spatial Iterated Prisoners Dilemma, *Proc. R. Soc. B* **259**, 77–83.

[132] Ferriere, R. & Michod, R. [1996]. The Evolution of Cooperation in Spatially Heterogeneous Populations, *Am. Nat.* **147**, 692–717.

[133] May, R. M. [1995]. Necessity and Chance: Deterministic Chaos in Ecology and Evolution, *Amer. Math. Soc.* **32**, 291–308.

[134] Comins, H. N. & Hassell, M. P. & May, R. M. [1992]. The Spatial Dynamics of Host-Parasitoid Systems, *J. Animal Ecol.* **61**, 735–748.

[135] Sole, R. V. & Valls, J. [1992]. Spiral Waves, Chaos and Multiple Attractors in Lattice Models of Interacting Populations, *Phys. Lett. A* **166**, 123–128.

[136] Szabo, G. & Fath, G. [2007]. Evolutionary Games on Graphs, *Phys. Rep.*. **446**, 97.

[137] Helbing, D. & Yu, W. [2008]. Migration as a Mechanism to Promote Cooperation, *A. C. S.* **11**, 641–652.

[138] Sinervo, B. & Lively, C. M. [1996]. The Rock-Scissors-Paper Game and the Evolution of Alternative Male Strategies, *Nature* **380**, 240–246.

[139] Burrows, M. T. & Hawkins, S. J. [1998]. Modeling Patch Dynamics on Rocky Shores Using Deterministic Cellular Automata, *Mar. Ecol. Prog. Ser.* **167**, 1–13.

[140] Szabo, G. & Czaran, T. [2001]. Defensive Alliances in Spatial Models of Cyclic Population Interactions, *Phys. rev. E* **63**, 1–13.

[141] Szabo, G. & Czaran, T. [2001]. Phase Transition in a Spatial Lotka-Voltera Model, *Phys. Rev. E* **63**.

[142] Frey, E. [2010]. Evolutionary Game Theory: Theoretical Concepts and Applications to Microbial Comunities, *Physica A* **389**, 4265–4298.

[143] Szamado, S & Szalai, F & Scheuring, I. [2010]. The Effect of Dispersal and Neighbourhood in Games of Cooperation, *J. Theor. Biol.* **253**, 221–227.

[144] Shakarian, P & Roos, P. & Johnson, A. [2012]. A Review of Evolutionary Graph Theory with Applications to Game Theory, *Biosystems* **2**, 66–80.

[145] Allen, B. & Traulsen, A. & Tarnita, C. & Nowak, M. A. [2012]. How Mutation Affects Evolutionary Games on Graphs *J. Theor. Biol.* **299**, 97–105.

[146] de Andrade, P. R. & Monteiro, A. M. V. & Camara, G. & Sandri, S. [2009]. Games on Cellular Spaces: How Mobility Affects Equilibrium*J. Artificial Societies and Social Simulation* **12**

[147] Cameron, D. & White, A. & Antonovics, J. [2009]. Parasite-Grass-Forb Interactions and Rock-Paper-Scissor Dynamics: Predicting the Effects of the Parasitic Plant Rhinanthus minor on Host Plant Communities *J. of Ecol.* **97**, 1311–1319.

[148] White, A. & Watt, A. D. & Hails, R. S. & Hartley, S. E. [2000]. Patterns of Spread in Insect-Pathogen Systems: the Importance of Pathogen dispersal *Oikos.* **89**, 137–145.

[149] White, A. & Begon, M. & Bowers, R. G. [1996]. Host-Pathogen Systems in a Spatially Patchy Environment *Proc. R. Soc Lond.* **263**, 325–332.

[150] Zimmer, C. [2000]. *Parasite Rex*. The Free Press.

[151] Freedman, L. [2013]. *Strategy: A History*. Oxford University Press.

[152] Boots, M. & Sasaki, A. [1999]. ”Small Worlds” and the Evolution of Virulence: Infection Occurs Locally and at a Distance *Proc. R. Soc Lond.* **266**, 1933–1938.

[153] Strauss, W. A. [1992]. *Partial Differential Equations: An Introduction*. John Wiley and Sons.

[154] Pollock, G. & Dugatkin, L. A. [1992]. ”Reciprocity and the Evolution of Reputation *J. Theor. Biol.* **159**, 25–37.

[155] Packer, C. [1977]. Reciprocal Altruism in Papio anubis *Nature* **265**, 441–443.

[156] Wilkinson, G. [1984]. Reciprocal Food Sharing in Vampire Bats *Nature.* **308**, 181–184.

[157] Milinski, M. [1987]. TIT FOR TAT in Sticklebacks and the Evolution of Cooperation *Nature* **325**, 433–435.

[158] Dugatkin, L. A. [1999]. *Cheating Monkeys and Citizen Bees*. The Free Press.